VI. *The Development of* Echinus esculentus, *together with some points in the Development of* E. miliaris *and* E. acutus.

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[Plates 7–16.]

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The investigations which form the subject of the present paper form the natural sequel to my paper on the development of *Asterina gibbosa* (see (15) in List of Works referred to, p. 133), which appeared in 1896. In the last-named work a complete account was given of the way in which the body of an asterid with all its organs is fashioned out of the body of the larva, and some important conclusions on the subject of the phylogeny of the Echinodermata were suggested by the results then obtained.

It has long been my desire to supplement the work done on a typical asterid by a similar study of the development of an echinid, not only because I desired to obtain such confirmation of the facts observed in the case of *Asterina gibbosa*, as would convince those of my colleagues who remained sceptical as to the interpretations

placed by me on the phases of asterid development, but also because, whilst the external features of the development of the Echinoidea were well known, our ignorance as to the main course of the development in so far as it affected the internal organs was very great indeed. In the present paper a fairly exhaustive account is given of the building up of the body of the adult sea-urchin out of that of the larva, and any objections which might be urged against the selection of *Asterina gibbosa* as a type on account of its modified and shortened development do not apply in the case of *Echinus esculentus*, the development of which is in all respects perfectly normal. I may so far anticipate the general result of the paper as to say that the conclusions arrived at from the investigation of the development of *Asterina gibbosa* are fully confirmed by the study of the development of *Echinus esculentus*.

Previous Work.

The larvæ of the Echinoidea were first of all discovered in the plankton by Johannes Müller (19), by whom they were termed "p l u t e i," on account of their fancied resemblance to a painter's easel, since they had a small compact body from which long arms or processes extended outward like the legs of an easel.

The name was, indeed, first bestowed on the larva of an ophiurid, the nature of which was not recognised, and which was termed *P l u t e u s p a r a d o x u s*. Later it was extended to the larvæ of the Echinoidea, which Müller discovered soon afterwards. As the larvæ of Ophiuroidea and Echinoidea differ in some very important respects from one another, and indeed are in each case more nearly related to the larvæ of the Asteroidea than to each other, the employment of the same name to designate two quite different types of larvæ is misleading and unfortunate. Mortensen (18), in his recent review of the echinoderm larvæ, has suggested the names e c h i n o p l u t e u s and o p h i o p l u t e u s for the larvæ of Echinoidea and Ophiuroidea respectively, and the name *echinopluteus* will be used throughout this paper. Johannes Müller described eight or nine types of echinopluteus, one of which is certainly to be identified with the larva of *E. miliaris*. The stages which he observed ranged from the four-armed larva to the larva which was just about to metamorphose, in which the first tube feet and spines of the adult were already formed, and he drew the conclusion that he was dealing with the larva of an echinoid, from the fact that in the suckers of these tube feet were embedded calcareous plates. In his figures and descriptions, Müller invariably placed the posterior pole of the larva upwards and the præoral lobe downwards, so that it is necessary to reverse his orientation in order to get a correct idea of the natural relationships of the parts of the larva. His description of the external features of the development is beautifully exact, and he made the discovery that the future oral disc of the Echinus develops on the floor of a pit of invaginated skin, the opening of which becomes closed.

About the same time KROHN (13) observed the early stages in the development of the egg, which he succeeded in artificially fertilising. He saw the formation of the alimentary tract by invagination and noted the uniform covering of cilia. The gap between the observations of KROHN and of MÜLLER was filled up by ALEXANDER AGASSIZ (1), who, on the one hand, succeeded in carrying on the rearing of artificially fertilised eggs of the American Sea-urchin, *Strongylocentrotus droëbachiensis*, to the development of a typical echinopluteus larva, and, on the other hand, obtained, by the use of the tow-net, a complete series of the later stages, so that in this way for the first time a complete history of the changes in external form undergone by a single species was obtained.

Under the name of W a t e r - t u b e, AGASSIZ described the cœlom of the larva, and he observed its origin from the gut. Already before this time in this and other classes of Echinodermata the formation of the cœlom had been described by METSCHNIKOFF (17), who called it the vaso-peritoneal vesicle, and who fully recognised its origin from the gut and the fact that it gave rise to the water-vascular system of the adult, a point which AGASSIZ could not observe.

In 1882 two pupils of Professor BROOKES, of Baltimore, Messrs. COLTON and GARMAN, published an account of the external features of the development and metamorphosis of Arbacia, in a paper which was inaccessible to me. It is, however, summarised by Professor BROOKES in his 'Handbook of Invertebrate Zoology' (3), with the addition of observations of his own, and the summary contains a detailed account of the external features of the metamorphosis.

In 1889 BURY (4), who had already published an exhaustive account of the development of *Antedon rosacea*, described a series of stages in the development of Echinoidea, based on plankton material. In this paper for the first time the division of the first formed cœlomic vesicle into anterior and posterior portions was described, and BURY interpreted this phenomenon as an indication of a previous metameric segmentation in a bilateral ancestor of the Echinodermata. He pointed out that the water-vascular rudiment is a development from the anterior cœlomic vesicle. He also discovered the right water vascular rudiment, but failed to recognise its nature, and termed it the d o r s a l s a c, and asserted that it was rhythmically contractile, In 1892 THÉEL (26) published, in a beautiful monograph on the development of *Echinocyamus pusillus*, a complete account of the external features of the development of the species, together with an account of the method by which he had been able to rear the larva throughout the whole of its free-swimming life until it had completed its metamorphosis. Finally, in 1896, BURY published a second paper on the "Metamorphosis of Echinodermata" (5), in which for the first time he applied the method of sections to the investigation of the structure of the echinoplute. In this paper he describes the metamorphosis in detail, and points out that the young urchin is at first devoid of an anus and without the second or recurrent coil of the intestine. He describes the origin of the ampulla of the stone-

canal from the anterior cœlomic cavity of the left side, and the growth of the left posterior segment of the cœlom so as to completely encircle the h y d r o c œ l e or rudiment of water-vascular system. He qualifies his former statement about the pulsation of the dorsal sac, and states that only the floor is contractile. From the year 1892 onwards HERTWIG, DRIESCH, HERBST, and many other observers have studied the early development of Echinoidea under abnormal conditions, not primarily with a view of extending our knowledge of the Echinodermata, but with the object of investigating the general laws of development. Since a well-grown female urchin contains about 20,000,000 eggs, it will be seen how admirably this group is suited for the purposes of experimental embryology. Incidentally, however, a number of facts have transpired which are of interest to the special student of Echinodermata, amongst the more important of which we may mention DRIESCH'S discovery that the cells of the blastula stage are at first potentially alike (8); that is to say that any sufficiently large fragment of the blastula, from whatever region it is taken, will round itself off and pursue a normal development, whereas after the mesenchyme has been formed this is no longer possible, the cells of the animal pole being unable to form a gut; and HERBST'S discovery (12) that by altering the chemical constitution of the water the gut may develop outwards instead of inwards, so that the process of invagination is due to the existence of a lesser pressure in the interior of the blastula than outside.

It will therefore be seen that, at the time the investigations recorded in this paper were commenced, we possessed an exhaustive account of the developmental processes which occurred during the first few days of larval life, a fairly coherent account of the external features of the larva throughout the entire period of the development, and the scantiest notices as to the internal changes which occurred after the first few days of development and as to the relation of the organs of the larva to those of the adult.

It is the aim of the present paper to present a full and thorough description of the steps by which the body of the adult is built up out of that of the larva, a task which has not been heretofore accomplished.

Methods Employed.

The first difficulty which was encountered was that of obtaining an adequate supply of material. It was for long deemed an impossibility to rear the larvæ for more than a few days. AGASSIZ on one occasion during cold weather managed to keep some alive for 3 weeks, but in most cases they died in a much shorter period (1). When the late Professor LUDWIG, of Bonn, was looking for a suitable type on which to commence an investigation of the manner in which the body of an adult echinoderm is built out of that of the larva, he abandoned all the species with typical free-swimming larvæ, and selected *Asterina gibbosa* (14) with its shortened development

and a yolky egg as the type for study, since in this case alone could he obtain the necessary supply of material of all stages in sufficient abundance. Since that time, as has been mentioned above, THÉEL published the method by which he reared the larvæ of *Echinocyamus pusillus* through the whole period of their development; but it is not clear from his paper whether many or few of his larvæ survived, and attempts to repeat his experiments in the Naples Aquarium resulted in failure.*

For the purposes of this paper it was, however, necessary to obtain the later stages of the echinopluteus and the stages of the metamorphosis in large numbers, and, after many failures, a method of accomplishing this was discovered. The material was obtained in the laboratory of the station of the Marine Biological Association, Plymouth, England, and I have here to express my warmest thanks to the director, Mr. E. J. ALLEN, who in the most generous manner placed at my disposal all the apparatus of the station during my sojourn there in the years 1898 and 1899. It has been my lot on various occasions to visit different biological stations, and I can confidently state that for facilities for research the station at Plymouth is unsurpassed; its only drawback being the contamination of the inshore water by the drains of the town, a defect which is now avoided by an arrangement by means of which water is brought in from a distance of several miles from the shore. To Mr. E. T. BROWNE, B.A., my warmest thanks are also due, for the kindness with which he placed his valuable experience in the rearing of marine animals at my disposal.

The method of obtaining material finally adopted is described below:—

Perfectly ripe males and females were selected for the purposes of experiment. They were not by any means easy to obtain; in the months of May and June one was lucky if one obtained a single ripe pair out of a haul containing over a hundred specimens. It is possible from almost any female to obtain some eggs which are capable of fertilisation; but in the case of *Echinus esculentus*, at any rate, the larvæ which result therefrom are more or less pathological, and can only be kept alive for a few days. The fertilisation of the eggs was effected in large, shallow glass dishes containing water, which, like all the water subsequently used in the cultures, had been brought from a long distance from shore. A very small amount of spermatozoa was added to the water, just sufficient to cause a very slight opalescence, and the ripe eggs were then added in sufficient quantity to cover the bottom in a single layer. The eggs were allowed to pass through a piece of Bolton silk, the meshes of which, as experience had shown, were of sufficient size to allow ripe eggs to pass through whilst preventing the passage of pieces of ovarian tissue and of unripe eggs. Unripe eggs

* Since the MS. of this paper was sent in for publication, GRAVE has published a preliminary account of the development of the Clypeastroid *Mellita testudinata* ("Some Points in the Structure and Development of *Mellita testudinata*," by CASWELL GRAVE, Ph.D., 'Johns Hopkins Univ. Circ.,' No. 157), and in a private letter to me he has described his method of rearing the larvæ. Mr. DONCASTER, of King's College, Cambridge, has also written announcing his success in rearing the Neapolitan species of regular sea-urchin.—*November* 6, 1902.

are surrounded by a thick glassy membrane which renders their diameter greater than that of the ripe eggs. The contents of the dishes were now vigorously stirred and allowed to settle. After about 20 minutes the water containing the spermatozoa was decanted off and replaced by clean sea-water. After the expiration of about 24 hours almost all the eggs had transformed themselves into free-swimming blastulæ, which had risen to the surface of the water, and could be decanted into the regular culture jars.

The jars used were about 2 feet high, and contained about 2 gallons of water. They were shaded from the direct sunlight, which is fatal to the larvæ, by being covered on the exposed side with black paper. They were protected from dust and evaporation by glass covers, and the aëration was provided for by introducing a small quantity of green filamentous alga. Often indeed this was rendered superfluous by the development of a film of alga on the sides of the jar from spores contained in the water. Each jar was provided with a Browne plunger. This invaluable piece of apparatus, which is the joint invention of Mr. ALLEN and Mr. BROWNE, consists of a glass plate fixed at right angles to a rod which passes through a hole in the centre of it, and which is secured by flattening out and enlarging the end under the blow-pipe. The other end of the rod is bent into a hook to which a piece of string is attached, and by this it is suspended from one arm of a light wooden balance. To the other arm of the balance a vessel is suspended which is slowly filled by water dripping from a tap, and intermittently rapidly emptied by a siphon of large bore which passes through a hole in the bottom. By means of suitable counterpoises the weight of this vessel is so adjusted that when full it is just able to pull up the horizontal plate in the culture jar, whereas when it has been emptied by the siphon, it is pulled up in turn by the plate as this sinks back to its original position. The consequence of this arrangement is that about twice a minute the water in the culture jar is gently agitated by the passage through it of the horizontal plate, and in this way the formation of a surface film of bacteria is prevented and the various layers are thoroughly mixed; some of the bottom water was siphoned off every day or two and replaced by clean sea-water; the action of the plunger being suspended during this process, and the larvæ allowed to come to the top. In such jars the larvæ lived and developed in perfect health for about a fortnight; and in one case, after such a culture had been proceeding for nearly 3 weeks, an approximate count showed that it contained nearly 700 healthy larvæ. This was in 1898, when the water contained a large number of unicellular algæ on which the larvæ fed; and in the same year a culture jar which must have contained at least 2000 larvæ of *Echinus miliaris*, was kept in a healthy state for a month, but the larvæ, although showing no signs of unhealthiness, did not develop beyond the four-armed stage. The first indication of unhealthiness in these larvæ is an inequality in the development of the arms, which causes a loss of perfect bilateral symmetry; the protoplasm of some of the arms, becomes gradually absorbed, leaving the calcareous rods embedded in them projecting freely. Perfectly healthy larvæ caught by the tow-net, if exposed to unfavourable conditions, will

exhibit this change in an hour or two. By keeping careful watch on the arms of the larvæ it is possible to note the first sign of unhealthiness, and thus to select only perfectly healthy specimens for the purposes of culture.

After a fortnight's sojourn in the culture jars above described, the healthiest larvæ were transferred to larger culture jars containing 10 gallons of sea-water and fitted like the smaller ones with covers and Browne plungers, and in these the development was completed in about 4 weeks or more. Only 150 larvæ were placed in each jar, and about one-third of the water was siphoned off and replaced by clean water daily. In this way an abundant supply of material of the later stages, and the stage of metamorphosis, was obtained.

The period of development at which the larvæ were transferred to the larger jars coincided roughly with the appearance of what is called the "echinus-rudiment." This consists of two structures which become closely opposed, but which were originally quite separate from one another. On the one hand there is the hydrocœle rudiment of the water-vascular system of the adult, and on the other an ectodermic pit, the floor of which comes into contact with the hydrocœle. During the sojourn of the larvæ in the larger culture jars this "echinus-rudiment" continually increases in size till it occupies the whole left side of the larva, and then metamorphosis occurs. If from any cause, such as neglect to add sufficient fresh sea-water to the culture jars, there is an insufficient supply of food, the echinus-rudiment ceases to develop, and may even become entirely absorbed without the larvæ showing any other sign of unhealthiness. It may even show on the right side the pedicellariæ and spines belonging to the aboral surface of the adult, whilst on the left no trace of tentacles or spines can be seen.

It will readily occur to the reader that it would have been a better plan to have selected a certain number of blastulæ or very young echinoplutei, and have transferred them at once to the larger culture jars. As a matter of fact this plan was tried, but it resulted in failure, as nearly all the larvæ died. The explanation of this curious fact which suggests itself to me is, that the hardiest larvæ can only be selected by subjecting them to a fairly severe struggle for existence during the first weeks of their existence. The survivors of this struggle are then exceptionally vigorous individuals, and capable of undergoing their further development without further trouble. This idea is confirmed by the observation that some of the hardiest larvæ were obtained from a culture in which, owing to the overcrowding of the eggs in the dish in which fertilisation was effected, only about one-tenth of the number developed.

The foregoing observations suggest that the great difficulty in rearing the larvæ is not the supply of oxygen, but the supply of food. In 1898 when unicellular algæ abounded in the water, the rearing of the echinoplutei was much easier than in 1899 when these were scarce.

It seems probable that similar considerations will apply to the case of the

larvæ of animals, such as fish, crabs, lobsters, &c., which are of economic importance.*

The larvæ were preserved in osmic acid, which was added to the sea-water in which they lived; they were left in the mixture until they had acquired a deep brown colour. From this they were transferred to Müller's fluid for a period of at least 24 hours, but a longer period inflicted no injury. Some which had remained for over a mouth in Müller's fluid gave excellent results. From the Müller's fluid they were transferred to 30 per cent. alcohol, and thence by gradual changes to 90 per cent., in which they were preserved. For purposes of section-cutting they were embedded in celloidin dissolved in a mixture of four parts of absolute alcohol and one part of ether; this proportion is important to observe, for if they be imbedded in celloidin dissolved in equal parts of absolute alcohol and ether, such as is usually employed in the preparation of sections of vertebrate tissues, it will be found that their delicate tissues are torn by the violent osmotic currents which are set up. The celloidin was congealed by pouring chloroform over it, the block containing a larva was then cut out, and *immersed for a second or two in clean absolute alcohol*, then transferred to a watch-glass full of clean chloroform with chips of hard paraffin immersed in it. The watch-glass was then placed in a thermostat standing at a temperature of 58° C., and in an hour all the chloroform had completely evaporated and the celloidin block was left embedded in the paraffin.

The immersion of the celloidin block for a moment or two in absolute alcohol before transferring it to the thermostat, is for the purpose of removing any traces of water which may be present in the chloroform. If this precaution be neglected the celloidin when heated is apt to become hard and opaque and utterly impossible to cut, instead of assuming a cheesy consistence and remaining translucent as it normally does.

The sections were cut parallel to three directions, viz., (*a*) parallel to the anterior surface of the larva, termed in the description of the plates *horizontal*. (*b*) Transverse to the length of the larva. (*c*) Parallel to the median sagittal plane of the larva, and were in most cases five μ thick. They were in all cases mounted on hot water to flatten them. The paraffin was dissolved off in xylol, and the slides were next placed for half a minute in oil of cloves, which extracted the celloidin; a longer sojourn tended to loosen the sections. They were then placed for 5 minutes in 90 per cent. alcohol, and then gradually brought into alcohol of the same strength as that in which the staining fluid was dissolved. It is important to avoid placing

* Since this paper was sent in for publication, CASWELL GRAVE'S paper (see footnote on p. 289) on *Mellita* has appeared. In a letter to me he explains that he discovered the special diatom on which the larvæ fed, and by supplying them with this in quantity he was able to hurry on the development. This result appears to be of great importance, and to confirm the conclusion arrived at in this paper.—*November* 6, 1902.

the slides in absolute alcohol after they have been in xylol, since in this fluid some sections are very liable to be detached from the slide. After the slide has been in oil of cloves and 90 per cent. alcohol, the sections are so firmly fixed that they will stand any treatment whatever. The staining fluid which gave the best results was a weak solution in water of Delafield's hæmatoxylin, followed in some cases by the alcoholic solution of eosin. The excess of stain was of course extracted in the ordinary way with acid alcohol, and any trace of acid remaining after rinsing the slide in 70 per cent. alcohol was removed by exposing the slide to vapour of ammonia. Sections treated in this way show no signs of fading after 3 years. It was found of advantage to immerse the slide in borax-carmine for 24 hours before exposing it to the hæmatoxylin. No stain is absorbed, but the subsequent staining by hæmatoxylin was facilitated.

The use of osmic acid followed by Müller's fluid as the sole fixing agent was dictated by several considerations, the principal one being the excellent results which this method had yielded in the case of the larvæ of *Asterina gibbosa*. Osmic acid, as has been pointed out by histologists like BETHE and BÜTSCHLI, is the best preservative for retaining in dead protoplasm the structures which have existed during life. Müller's fluid completes the hardening process and at the same time slowly decalcifies, but so slowly that the CO_2 produced seems to be at once dissolved in the fluid, and no trace of the distortion of the tissue owing to the accumulation of this gas was ever seen. This is a point of great importance in the case of Echinodermata, in which there is so much calcareous matter, and whose tissues are so delicate. The ordinary fixing fluids, such as corrosive sublimate, Fleming's fluid, Perenyi's fluid, and so on, are strongly acid, and are therefore unsuitable in the case of the Echinodermata. The great disadvantage in the employment of osmic acid followed by Müller's fluid is that they make tissues very brittle, especially those composing the echinus-rudiment, which is just the part which it is specially desired to examine. It was necessary to use exceedingly sharp razors to obtain good sections, but these when obtained were so clear and diagrammatic in every detail as to compensate for the extra labour involved. Before passing on to describe the development in detail, I may append a short tabular scheme of the succession of events, which will be useful for reference ; the times being, of course, reckoned from fertilisation.

Blastula fully formed and swimming at the surface	1 day.
Gastrula, completed	2 days.
Cœlom, formed	$2\frac{1}{2}$–3 „
Stomodæum meets œsophagus	$3\frac{1}{2}$–4 „
Madreporic pore formed	4 „
Third pair of arms appear	7–8 „
The left cœlomic sac transversely segmented	9 „
The left hydrocœle formed	10–11 „
The right cœlomic sac transversely segmented	12 „
The anterior ciliated epaulettes formed	13–14 „

The invagination which will form the oral disc of the Sea-urchin makes its appearance	14–15 days.
The right hydrocœle (or madreporic vesicle) formed.	17–18 „
The fourth pair of arms formed	18–20 „
Formation of the epineural folds covering the oral disc	22–24 „
Formation of the first three pedicellariæ	24–26 „
Formation of the rudiments of Aristotle's lantern and of the posterior ciliated epaulettes	26–28 „
Formation of the spines of the adult	33–36 „
The amniotic cavity acquires an opening to the exterior, and the tube feet exhibit movement	36–40 „
Metamorphosis	42–50 „

Comparison of the Early Stages in the Development of Echinus esculentus, Echinus acutus, *and* Echinus miliaris.

Besides the larvæ of *Echinus esculentus* attempts were made to rear those of the two other species of Echinus which are common at Plymouth, viz., *E. miliaris* and *E. acutus*. In the case of *E. miliaris* a fairly complete series of stages were obtained which were used to confirm the observations made on *E. esculentus*, and to bridge over one or two gaps which through insufficient material were found in the series of stages of *E. esculentus* in my collection of the larvæ. In a previous paper (16) I have described the main peculiarities of the echinopluteus of *E. miliaris*, which differs markedly from that of *E. esculentus*. I may here remind the reader that it is a smaller larva, and of a more flattened shape in an antero-posterior direction than the larva of *Echinus esculentus*; that it only develops one series of ciliated epaulettes, and that the characteristic green pigment of the adult first makes its appearance at the base of each of these epaulettes (compare figs. 7 and 9, Plate 8). The just metamorphosed *Echinus miliaris* is also distinguishable from that of *E. esculentus* by the fact that in the former case there is a pair of fully developed tube feet in each radius in addition to the unpaired one, whereas in the latter case this is not so (compare figs. 8 and 10, Plate 8). In the case of *Echinus acutus* I was not successful in rearing the larvæ for more than 10 days.

A comparison of the early stages of development of these three species shows that from the start they are distinguishable from one another, although the larvæ of *E. esculentus* and *E. acutus* very closely resemble one another, differing principally in size, whereas that of *E. miliaris* is markedly different from them both (compare figs. 12 and 13, Plate 7). The blastula stage in the last named is more elongated and thinner walled, and this elongation is shown by the succeeding gastrula and echinopluteus stages to be due to an increase in size of the forehead or præoral portion of the larva. This enlarged forehead, which is evidently a reminiscence of the præ-oral lobe of the asterid larva, is visible throughout the later development as a lobe overhanging the mouth (see fig. 6, Plate 8). The relationship of the larvæ of

the three species is therefore exactly the relationship of the adult forms, since *E. esculentus* and *E. acutus* are closely allied species, whereas *E. miliaris* has by some authorities been removed to another genus (Psammechinus).

The Development of the Echinopluteus of Echinus esculentus.

It has already been mentioned when reviewing the work of other investigators on the development of the Echinoidea, that we possess an exhaustive account of the earliest stages of development, and it might seem mere waste of time to refer to them here. There are, however, one or two questions concerning them which remained unanswered, and on these an endeavour was made to obtain additional light by means of sections. In 1886, SEDGWICK (20), in describing the early development of Peripatus, made the suggestion that in the eggs in which apparently complete cleavage takes place, the segments may, as in Peripatus, be organically connected at the point of contact. In conversation with me he put forward the further idea that possibly the apparently hollow blastula, wherever it occurs, is really traversed by strings of protoplasm, and that the blastocœle or segmentation cavity is really to be regarded as consisting of a few enormous vacuoles essentially similar in character to the vacuoles found in ordinary protoplasm. With a view of testing these hypotheses, sections were made of various stages in the segmentation and of the blastula (see fig. 12, Plate 9), and it at first seemed as if SEDGWICK's ideas were confirmed, for between the various segments of the egg a deeply staining reticulum was found, and the interior of the blastula was filled up with a dense reticulum. When, however, the living blastula (fig. 15, Plate 9) was examined under a high power nothing of this reticulum could be observed, but in place thereof certain protoplasmic strings were observed connecting the first-formed mesenchyme cells with each other and with the wall of the blastula. When the fact is borne in mind that anything which, like Müller's fluid, contains chromic acid, and even alcohol itself, are known to precipitate from proteid solutions a coagulum which has often a reticulate form, we shall be driven to conclude that in the interior of the blastula and in the crevices between the segments of the egg there is a fluid proteid which may be compared to the yolk in larger eggs. Whether this fluid proteid is in any essential point different from living protoplasm—whether in other words it is the seat of metabolism—is a question whose answer we do not know. As development proceeds, however, this proteid solution becomes thinner and thinner, as will be seen by a glance at figs. 13 and 14 (Plate 9), which portray sections through the gastrula stage and the stage in which the cœlom is formed respectively. In fig. 14, the coagulum has almost if not quite disappeared, for many of the strings traversing the blastocœle which are shown in that figure do not consist of coagulum, but can be seen in the larva whilst it is living. HERBST has shown (12) that by altering the composition of sea-water in which the blastulæ are living, and in

consequence altering the relations between the osmotic pressure inside and outside of the blastula, the archenteron may be made to develop outwards instead of inwards, and produce what he calls an exogastrula. It is clear therefore that the process of invagination is due primarily to an increase in the cells on one side of the blastula, and that the growing part seeks relief from lateral pressure by bending inwards or outwards in the direction of least pressure. It appears to me that the thinning of the solution of proteid in the blastula cavity is in all probability the antecedent cause of invagination.

On the 3rd day the cœlom is separated from the apex of the archenteron (see fig. 14, Plate 9), and is at first a single vesicle as in the case of *Asterina gibbosa*. It almost immediately divides into right and left portions, and at the same time the gut becomes differentiated into an œsophagus, stomach, and intestine, separated from one another by constrictions, whilst the stomodæum makes its appearance as a shallow pit. The blastopore, of course, persists as the anus (see Plate 7, fig. 3). The larva has now a concave ventral surface and a strongly humped dorsal one; and the edge limiting the dorsal surface projects further forward in front than behind. It is in this projection that the stomodæum makes its appearance, and for this reason it will be called the oral lobe of the larva.

Round the edge of the ventral surface the longitudinal ciliated band, the organ of locomotion, is making its appearance. This band, as is well known, becomes pulled out into processes which constitute the characteristic "arms" of the echinopluteus larva. Of these, following MORTENSEN'S notation (18), the first to appear are the postero-dorsal pair, which are distinct on the 3rd day, and the next are the antero-lateral pair, which make their appearance on the 4th day. Not until the 7th or 8th day do any further arms show themselves, and the four-armed echinopleuteus is thus the characteristic form of the young larva in this genus as in all the other genera which have been examined.

Besides the longitudinal ciliated band, the larva possesses a ciliated loop crossing the dorsal surface of the stomodæum near its opening, and on the ventral side projecting like a V into the œsophagus. This band, known as the adoral ciliated band, has been compared by GARSTANG (10) to the endostyle of the Ascidians and Amphioxus. Now the endostyle of these animals is an organ belonging to the true endodermic gut, and it becomes therefore of interest to determine whether the adoral band is formed from the ectodermic stomodæum or from the endodermic œsophagus. The band is unfortunately not formed until, on the 5th day, the stomodæum has joined the œsophagus; but a careful comparison of horizontal sections through the larvæ immediately before the union of the stomodæum and œsophagus, and immediately after that event, leaves no doubt that the adoral band is formed from both ectoderm and endoderm (see figs. 16, 17, and 18, Plate 9).

This discovery places considerable difficulties in the way of comparing it with the endostyle, and an additional difficulty is created when we compare the functions of the two organs. That of the endostyle is to produce a cord of mucus which is worked forwards by the action of the cilia to the opening of the mouth, where it is torn into strings by the in-rushing current produced by the cilia lining the gill slits; object these strings serve as a net to entangle the organism contained in the water. The of the adoral ciliated band, on the contrary, is to sweep into the œsophagus any organisms which may have been brought into the neighbourhood of the mouth by the action of the longitudinal ciliated band. We may add that the adoral band is entirely independent of the longitudinal band, and not an inwardly projecting loop of it as GARSTANG supposes. From time to time a peristaltic movement of the œsophagus occurs, and the accumulation of food lying in its outer end is passed into the stomach. This peristalsis is due to semicircular bands of muscle surrounding the ventral half of the œsophagus, which are seen to be developed from the walls of the cœlomic sacs. (Compare fig. 20, Plate 9, where they are just developing, with fig. 29, Plate 10, a section taken from a much older larva, where they are fully formed. In older larvæ they completely encircle the œsophagus.) The dilatation of the œsophagus after contraction appears to be due to a contractile cord of cells given off from the anterior part of the cœlom on each side, and inserted in one of the calcareous rods supporting the antero-lateral arms.

In his work on the development of *Asterias pallida* (11), GOTO puts forward the revolutionary hypothesis that the Echinodermata really retained in the adult condition the bilateral symmetry of the larva, and that a plane passing through the madreporite and the opposite radius was identical with the median sagittal plane of the larva; in other words, that the primary madreporic pore is from the first median in position. This view was opposed to my observations (15) and to those of LUDWIG (14) in the case of *Asterina gibbosa*, and also to those of FIELD (9) on the larva of *Asterias vulgaris*; but it was of such far-reaching significance that it seemed most desirable to test it in the case of *Echinus esculentus*. In the larva of this animal on the 4th day a dorsally directed outgrowth (*p.c.*, fig. 19, Plate 9) from the left cœlomic sac is visible. This is the pore-canal, and on the next day it meets and fuses with the ectoderm (fig. 20, Plate 9), and thus the primary pore is formed as an organ belonging unmistakably to the left side.

Before this time the larvæ both of *Echinus esculentus* and of *Echinus miliaris*, if at all healthy, have developed a large amount of red pigment. Microscopic examination of the living larvæ shows that this pigment is contained in amœbocytes which are wandering outwards. They invade the ectoderm, and here appear to degenerate, for besides perfect amœbocytes, granules of pigment are often found embedded in the ectoderm. There is little doubt that the pigment is an excretory product in process of removal.

BURY'S two papers (4 and 5) are the only communications in which the transverse

division of the cœlomic sacs into anterior and posterior halves is described. This indication of metamerism in the larva has been generally received with scepticism. THÉEL remarks that he was unable to confirm it, and SPENGEL (25) rejects it. A transverse division was described by me in the larva of *Asterina gibbosa* (15), but it is rendered less striking by the occurrence of secondary perforations in the septum dividing the anterior and posterior portions of the cœlomic sac. Hence it was considered to be extremely desirable to thoroughly investigate this point in the larva of *Echinus esculentus*. An exhaustive study of larvæ ranging in age from 5 to 15 days enabled me to set aside all doubt on the subject, as a study of the sections figured on Plate 10 will show. As the larva grows beyond the stage it had attained at the age of 5 days, when the primary madreporic pore had just been formed, the cœlomic sacs grow backwards along the sides of the stomach (fig. 22, Plate 10); and at the same time the left one, about the middle of its length, enlarges and becomes thin-walled, forming the ampulla, into which the stone-canal opens (fig. 21, Plate 10). At the age of 8 days the left cœlomic sac divides into two just behind this enlarged portion (figs. 23 and 24, Plate 10), giving rise to a left anterior and a left posterior cœlom, and on the 9th day the enlarged ampulla becomes constricted into two portions, the anterior one of which remains as the definitive ampulla, whilst the posterior one is the left-hydrocœle, the rudiment of the water-vascular system of the adult (fig. 25, Plate 10).

The stone-canal (*st. c.*, text-figs. 1 and 2, fig. 32, Plate 11) is produced by the drawing out of the neck of communication between the ampulla and the hydrocœle as the latter migrates backward to take up a position on the ventral side of the stomach. At about the 12th day the right cœlomic sac becomes divided into anterior and posterior portions (fig. 27, Plate 10), but there is at first no sign of the formation of any homologue of the hydrocœle from the anterior half. During this time the third pair of arms has made its appearance; this is the pair called by MORTENSEN the post-oral (figs. 8 and 9, Plate 8). The re-entrant loop which the longitudinal band of cilia makes between the post-oral and the postero-dorsal arms is a deep and narrow one and within this loop close to its apex an invagination of the ectoderm takes place, just above the position which the left hydrocœle has assumed (*Ech.*, figs. 26 and 28, Plate 10). This invagination is the rudiment of the whole ambulatory surface, or, as we shall term it, the oral disc, of the future sea-urchin, and it becomes clearly marked between the 12th and 14th days.

Slightly later the anterior ciliated epaulettes are formed. These are horizontally placed crescentic bands of cilia, four in number, which are constructed off from the main ciliated band at the bases of the post-oral and postero-dorsal arms (a *cil. ep* fig. 5, Plate 7, and fig. 9, Plate 8). A formation of such epaulettes from the ciliated band was described by AGASSIZ in the case of *Strongylocentrotus dröebachiensis* (1). In a former communication (16) I asserted that the epaulettes were independently developed, but further observations have convinced me that AGASSIZ was

perfectly right. These epaulettes carry exceptionally powerful cilia, and on them as development proceeds more and more of the work of propelling the larva devolves.

At from the 16th to 17th days from the right anterior cœlom is developed a structure which I regard as the equivalent on the right side of the water-vascular rudiment—in a word, as the r i g h t h y d r o c œ l e. Since it is situated dorsally to the main portion of the right cœlomic sac, and at the same time nearer the median plane, it is impossible to show in any one section its true relations, and its development can only be satisfactorily studied in transverse sections. When the right anterior cœlom is traced backwards in such sections it is found to taper off into a narrow string of cells. This string in larvæ 16 days old extends to almost the mid-dorsal line of the œsophagus, and there ends in a thickening (fig. 30, Plate 11). This thickening becomes gradually separated from the string of cells (figs. 31 and 32, Plate 11), and forms a little solid nodule lying dorsal to the œsophagus beside the pore-canal. In this stage it was seen by BURY (5). Later it acquires a cavity (fig. 33, Plate 11), and persists throughout life as a perfectly closed thin-walled sac situated beneath the madreporic plate. BURY (5) calls it the dorsal sac, and compares it to the pericardium of the Tornaria larva and of Balanoglossus. In its origin, however, and its adult relations, it exactly corresponds to the sac in *Asterina gibbosa*, which I termed the right hydrocœle (15).*

This sac was shown to be the homologue of the left hydrocœle by the fact that in

* It is difficult to account for the pulsation which BURY (4) asserts that he has seen in this organ. In his later paper (5), however, he admits that it is only the floor of the sac which pulsates. I have never seen any pulsation in any part of the sac, nor is there any trace of muscle-fibres to be seen in its wall. There is, however, a layer of muscle-fibres surrounding the œsophagus, in which from time to time a peristaltic contraction takes place. Now, the floor of the right hydrocœle is closely opposed to the œsophagus at the sides, though it is raised up in the middle; and it seems to me to be probable that it was a passive movement of the hydrocœle caused by peristalsis in the œsophagus which misled BURY.

BURY'S theory has been revived by A. T. MASTERMAN ("The Early Development of *Cribrella oculata*," 'Trans. Roy. Soc. Edinburgh,' vol. 11). The development of this asterid is indeed extraordinary if MASTERMAN'S results are confirmed. The cœlom appears to arise as two separate vesicles from the archenteron, an anterior and a posterior. From the latter is derived the left posterior cœlom, regarded by MASTERMAN as a median organ; from the former, the anterior cœlom, the hydrocœle, and the right posterior cœlom. The larva is a highly modified one, and at no time possesses a mouth. On the strength of this abnormal and exceptional type of development, MASTERMAN is prepared to regard the right posterior cœlom (or, as he terms it, the epigastric cœlom) as equivalent to the right hydrocœle. I do not think that this revolutionary view, which regards the right and left posterior cœloms as metameres and not antimeres, and thus presupposes a fundamental asymmetry in the typical free-swimming larva, will meet with much favour. It is completely disproved by the occurrence of exceptional larvæ in *Asterina gibbosa*, in which the right hydrocœle is as well developed as the left, for there we can see the epigastric cœlom in its normal development side by side with two fully developed hydrocœles. CASWELL GRAVE (footnote, p. 289) has found that in *Mellita* the right hydrocœle develops from the right anterior cœlom and has a pore-canal. The only Echinoderm development hitherto described in which the cœlomic vesicles arise separately from the archenteron is that of *Antedon*, and in that case the epigastric cœlom arises from the posterior vesicle.—*November* 6, 1902.

certain abnormal larvæ it developed lobes exactly corresponding to those of the left hydrocœle. In the case of *Echinus esculentus* such larvæ were not found. Still we can assert that the "dorsal sac," or to use a purely non-committal name, the madreporic vesicle, originates from the posterior end of the right anterior cœlom exactly as the left hydrocœle originates from the hinder end of the left anterior cœlom; and the fact that it is a solid outgrowth, and not, as in the case of *Asterina gibbosa*, a hollow evagination, is correlated with the feeble development and narrow lumen of the cœlomic sacs in the echinopluteus, as compared with the larva of the asterid.

Reviewing the course of development so far, we see that the right cœlomic sac undergoes the same changes as the left, but that they are slower in making their appearance, and this agrees with what was observed in the case of *Asterina gibbosa*, and it is to the first indication of that preponderance of the organs of the left side which is one of the main factors in the development of Echinodermata (see text-fig. 1).

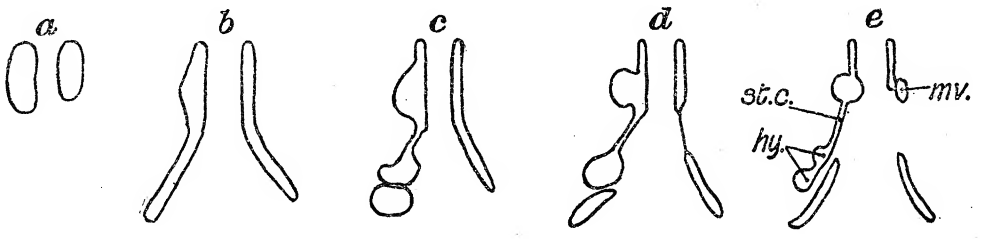

Fig. 1.—Five diagrams showing the changes undergone by the cœlomic sacs of the echinopluteus. *st. c.*, stone-canal; *hy.*, left hydrocœle; *mv.*, madreporic vesicle or right hydrocœle.

By the time that the right hydrocœle is fully developed, the posterior divisions of the cœlomic sacs have extended backwards along the sides of the stomach so as to almost meet each other at the posterior pole of the larva (fig. 28, Plate 10). The growth that takes place is mainly confined to their outer walls, which remain comparatively thick, whilst their inner walls appear to be passively stretched, since they consist of extremely attenuated cells. Transverse sections show that they are also extending in a dorsal-ventral direction (fig. 30, Plate 11), but they are still confined to the central zone of the stomach wall. At the same time the invagination destined to form the oral disc of the sea-urchin becomes more and more flask-shaped by the constriction of its opening (fig. 28, Plate 10), and a little later it is completely closed off from the exterior. Its cavity will be called the amniotic cavity. It has by this time come into close contact with the left hydrocœle, which has assumed a flattened pentagonal form; the somewhat projecting angles of the pentagon being the first indications of the radial canals, and unpaired tube-feet of the young sea-urchin (figs. 28, Plate 10, and 35, Plate 11). The left posterior cœlom sends forward a horn (*l'p'c'*, fig. 28) dorsal to the hydrocœle, which sweeps round it in a ring-fashion, meeting the main portion of the sac beneath;

again, in this point the development of *Echinus esculentus* recalls what occurs in *Asterina gibbosa*. The main difference in the case of *Echinus esculentus* is the comparatively early period of development at which the process of encircling the hydrocœle is completed. In *Asterina gibbosa* the hydrocœle is at first a hoop, which

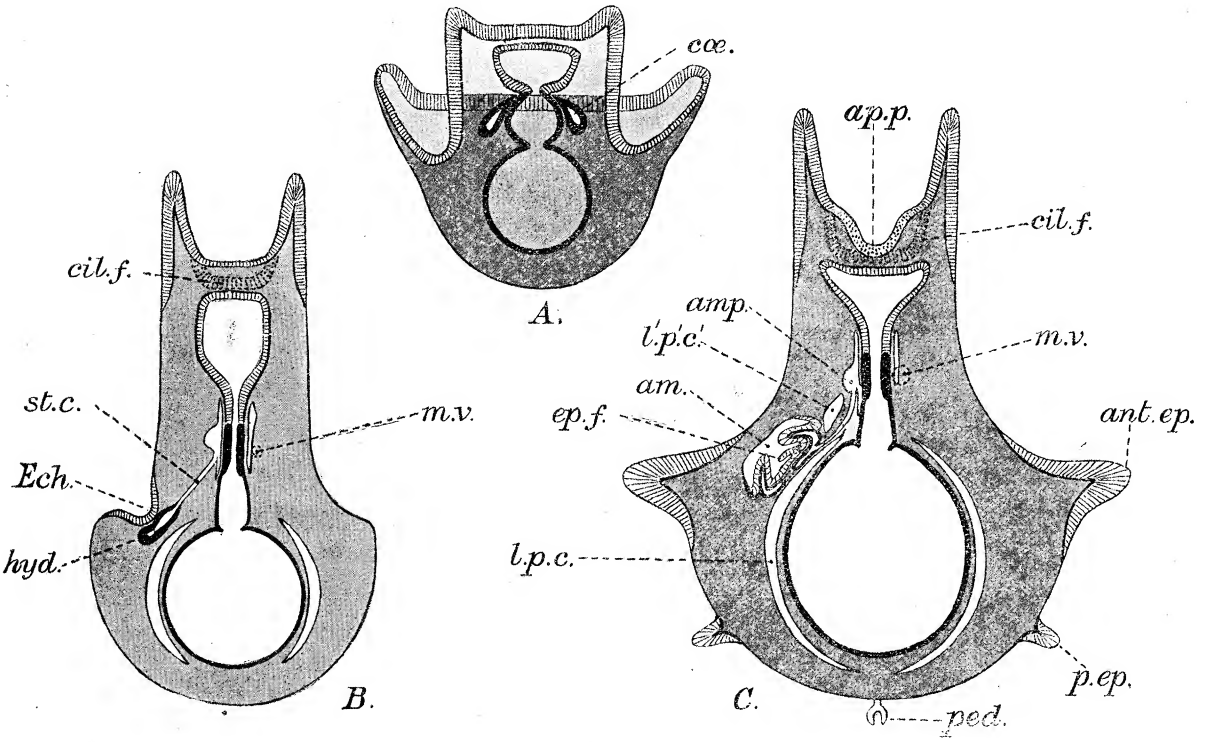

Fig. 2.—Three diagrammatic frontal sections through larvæ of different ages to show the development of echinopluteus. *A* represents an optical section, *B* and *C* actual sections. *A* through a larva 4 days old; *B* through a larva of 18 days; *C* through a larva 24 days old; *am.*, amniotic cavity; *ap.p.* apical plate; *cil.f.*, frontal cilia; the position of the ciliated band corresponds to the frontal loop of the Asteria larva. *Ech.*, invagination about to form oral disc of adult; *l.p.c.*, *l' p' c'*, the two horns of the left posterior cœlom; *m.v.*, right hydrocœle.

gradually becomes converted into a ring by the meeting of the ends, and the left posterior cœlom undergoes step by step the corresponding change, whereas in *Echinus esculentus* the hydrocœle is at first a disc, but almost immediately assumes the form of a complete ring, and the left posterior cœlom correspondingly rapidly assumes the form of a ring around it.* At about 20 days the fourth and last pair of arms make

* I could not with certainty determine how the ring-form is attained. In the preliminary account of this paper ('Proc. Roy. Soc.,' vol. 69) I stated that it was caused by the perforation of the disc by the œsophagus. This is a mistake, as I find by careful revision of my sections that the ring-form is attained much earlier. I believe, however, that it is formed as described for *Echinus miliaris* in a paper by Théel, of which I received a copy after the MS. of this paper was sent in. In that paper ("Preliminary Account of the Development of *E. miliaris*," 'Proc. Roy. Swedish Acad.,' vol. 28) he describes the hydrocœle as having at first a pentagonal form, but soon a small notch appears on the posterior border of this, which,

their appearance, and the echinopluteus may, in the case of *Echinus miliaris* at least, be said to have reached the summit of its development; the larva of *E. esculentus* has, however, still some changes in its outer form to undergo.

At about this time also in both species the larval nervous system makes its appearance. For a long time efforts have been made to find a nervous system in the Echinoderm larva, but without much success. SEMON described a nervous system in the larva of *Synapta digitata* (24), which consisted of two bands of cells running parallel with the main longitudinal portions of the ciliated band, and giving off fibres to them. His account of these structures is very unsatisfactory; nothing at all similar has been found in any other Echinoderm larva, and the subject requires re-investigation, for larval nervous systems in general do not consist of bands of cells but of neuro-epithelium. The apical plate and associated nervous tissue described by SEELIGER in the case of the aberrant larva of *Antedon rosacea* (23), accord with what we should expect to find in a type of larva in which histological differentiation was so feebly pronounced. The discovery of this nervous system, the first one in any Echinoderm larva of which a satisfactory account has been given, has led to the search for similar structures in the larvæ of other groups of the Echinodermata. In the larva of *Asterias vulgaris*, FIELD (9) described a thickening at the apical pole, but could find no fibrillæ, and in the larva of *Asterina gibbosa* (15) I was able to demonstrate a thin sheet of nerve fibrils underneath the epithelium forming the thickened edge of the præ-oral lobe, and in the echinopluteus of *Echinocyamus pusillus* (26), THÉEL described in the gastrula stage an apical thickening bearing stiff cilia, which he was inclined to compare with the apical plate of the Trochophore larva.

In commenting on THÉEL'S observations, I (16) pointed out that inasmuch as this thickening became later incorporated with the frontal portion of the ciliated band running on the præ-oral portion of the larva between the two præ-oral arms (see text-fig. 2), it could not be compared to the apical plate of the Bipinnaria or of the Tornaria larva of Balanoglossus, which occupied a position at the extreme anterior end of the larva where the frontal or præ-oral loop was given off, unless indeed the ciliated band of the echinopluteus was to be regarded as equivalent to that of the Bipinnaria *minus* the præ-oral loop. The thickening described by THÉEL is feebly marked in the gastrula and young larva of *Echinus esculentus*; traces of it, however, can be observed in figs. 14 and 16, Plate 9.

I despaired of finding any other representative of a larval nervous system than this, which since it exhibits no visible fibrils can hardly be considered a nervous system at all. By accident rather than design, when examining larvæ about to metamorphose, I discovered an exceedingly well-developed plate of neuro-epithelial tissue with a thick bed of fibrils at its base, situated at the extreme anterior pole

by the meeting of its edges, is made into a perforation of the pentagon, and so the ring-form is attained. In *Mellita*, according to GRAVE, the hydrocœle is for a long time an open hoop, as in the Asteroidea.—*November* 6, 1902.

of the larva, outside the ciliated band, and exactly corresponding in position to the apical plate of the Bipinnaria and Tornaria larvæ (*ap.*, fig. 37, Plate 11). In tracing the plate back to its origin, I discovered the first trace of it in larvæ 20 days old (*ap.*, figs. 34 and 36, Plate 11), as a thickening frequently slightly invaginated, and situated between the præ-oral arms. The fibrils extend in a transverse direction, and the main function of the structure seems to be to co-ordinate the two halves of the ciliated band (see text-fig. 3).

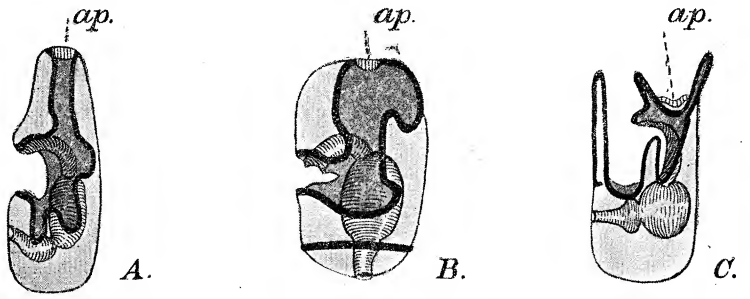

Fig. 3.—Three diagrams representing the side views of the Bipinnaria, the Tornaria, and the Echinopluteus larvæ respectively. *A* the Bipinnaria; *B* the Tornaria; *C* the Echinopluteus. The ciliated band is represented by a heavy line, and in the Echinopluteus the præ-oral loop of the ciliated band is very short. *ap.*, the apical nervous system.

The Development of the Echinus-rudiment in the Interior of the Larva.

From about the 21st day until just before the metamorphosis, the larvæ of *Echinus miliaris* do not perceptibly alter their outer form. Those of *Echinus esculentus*, however, about the 23rd day acquire a posterior pair of ciliated epaulettes (*p. cil. ep.*, fig. 9, Plate 8), which like the anterior epaulettes are simply portions of the main ciliated band cut off from the rest. They are derived from the re-entrant angles between the postero-dorsal and the præ-oral arms. Both anterior and posterior ciliated epaulettes continue to grow till they form just before the metamorphosis two practically continuous circles of ciliated epithelium surrounding the posterior pole of the larva. With this exception, however, the form of the larva 21 days old is very similar to that of a larva just about the metamorphose, and, as in the case of the larvæ of *Echinus miliaris*, the principal change which takes place between the 22nd and 40th day of development is the growth in size of the "echinus-rudiment." This as has been already explained is really a compound structure resulting from the co-adaptation of two originally quite independent structures, viz. (1) the middle division of the left cœlom or left hydrocœle, and (2) the floor of an ectodermic pit, which becomes flask-shaped, and eventually entirely closed off from the exterior forming a closed sac (fig. 38*b*, Plate 12). The cavity of this sac is the amniotic cavity. The Echinus-rudiment gives rise to the whole

ambulacral or actinal surface of the adult, and as it enlarges so does the amniotic cavity, till both together occupy the whole side of the larva (fig. 49, Plate 14).

At 20 days the rudiment seen in face is a pentagonal disc, with slightly projecting angles, which are the rudiments of the primary unpaired tube-feet. At about 22 days, alternating with these projections, there arise five ectodermic ridges (*ep. f.*, figs. 40 and 41, Plate 12), the free edges of which project inwards over the centre of the disc (fig. 41*b*), and at the same time extend laterally like overhanging eaves of a roof towards the corresponding edges of the neighbouring folds (fig. 40). If we call the projecting angles of the echinus-rudiment the radii, we may speak of these ridges as being inter-radial in position, and for reasons to be explained immediately we shall call them the epineural folds.

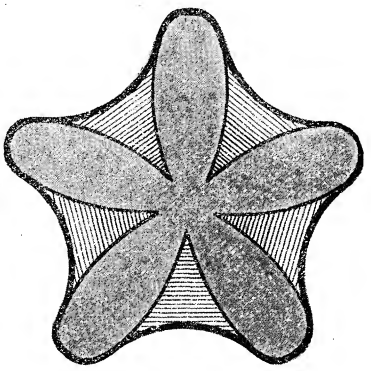

Fig. 4.—Plan of the Echinus-rudiment at about 24 days, viewed from the outside. The cross-hatched wedges are the epineural folds.

Very shortly afterwards, the free edges of these ridges meet each other both laterally and in the centre of the disc, and in this way is enclosed a central space running out into five short canals lying above the bases of the primary tentacles (*ep.*, fig. 43, Plate 12). These canals are the rudiments of the epineural canals of the adult, which lie superficially to the radial nerve cords, and we may term the central space into which they open the epineural space. It is a transient structure, and the sheet of tissue forming its roof will be spoken of as the epineural veil.

At about the 26th day evaginations of the outer wall of the left posterior cœlom are found projecting into the bases of the epineural ridges. At first there are only four of these, the fifth making its appearance about the 29th day (*d.s.*, fig. 42, Plate 12). These cœlomic pockets are the rudiments which give rise eventually to the masticatory apparatus known as Aristotle's lantern; from each originates a tooth and its supporting jaw, and so I have termed them dental-sacs.* They exactly

* This account of the origin of Aristotle's lantern has received confirmation both by GRAVE (see footnote, p. 289) and THÉEL (see footnote, p. 301) since the manuscript of this paper was sent in.—*November* 6, 1902.

correspond in position and origin to the five rudiments of the perihæmal system of canals described by me in the larva of *Asterina gibbosa* (15), and, as we shall see, from them are derived the radial perihæmal canals of the adult urchin. These cavities of the dental sacs become very soon closed off from the left posterior cœlom (fig. 43, Plate 12), and a small thickening in the outer walls of each indicates the first rudiment of the tooth. In *Asterina gibbosa* one of the corresponding rudiments is developed from the anterior cœlom, which in the larva of this form is very spacious; but the echinopluteus, at this age the left anterior cœlom or ampulla, is confined to the side of larval œsophagus, and does not extend to anywhere in the neighbourhood of the echinus-rudiment. During this time the angle of the hydrocœle, which are the rudiments of the first tube-feet, have been projecting further and further into the amniotic cavity (*t*, figs. 40, 41, and 42, Plate 12), their ends being at first rounded. By the time that the larva has attained an age of about 26 days, the first traces of histological differentiation, in the shape of nervous and muscular tissue, are observable in the Echinus-rudiment. These can be well seen in fig. 46, Plate 13, which was drawn under the magnification afforded by a Zeiss apochromatic oil-immersion lens. In the ectoderm of the Echinus-rudiment the nuclei have increased very much in number, and are disposed in several layers, and at the base may be seen two or three nerve fibrils, which can be traced into the nuclei; these constitute the first appearance of the adult nerve ring. At the same time some of the cells of the portion of the hydrocœle contained in the tentacle are beginning to become elongated; this is the first stage in the formation of the longitudinal muscles characteristic of that organ. In the later stage, represented in fig. 43, Plate 12, a thick bed of nerve fibrils intervenes between ectoderm and hydrocœle, and still later it can be seen that the cells of the body of the hydrocœle are developing into circular muscles (*musc.*, fig. 44*b*, Plate 13).

The epineural fold, which covers in the epineural spaces, is at first very thin, consisting simply of two opposed layers of ectoderm (fig. 41*b*); it soon, however, becomes much thicker,* these two layers being separated by an invading mass of jelly (fig. 46, Plate 13), into which at a later stage amœbocytes wander, which set up calcification, for, as is well known, in this fold are formed the so-called "ambulacral plates" of the adult.

By the time the larva has attained an age of 29 days, the unpaired tube-feet have acquired suckers at their free ends (fig. 43), and the rudiment of the tooth in the dental sac has grown so much that the whole structure becomes V-shaped in section (fig. 44*b*, Plate 13).

During this time other changes have been occurring. The formation of the posterior ciliated epaulettes has been already mentioned, but when the larva is about 24 days old the three first pedicellariæ make their appearance (*ped.* 1, *ped.* 2, *ped.* 3,

* This stage has been seen by THÉEL in his last paper (see footnote, p. 301).—*November* 6, 1902.

fig. 38, Plate 12). Of these, one (*ped.* 2, fig. 38*b*) is situated at the posterior pole of the larva, the other two on the right side, one dorsally and the other ventrally, but in the same transverse plane. Each pedicellaria makes its appearance as a little knob, or evagination of the ectoderm, the interior of which becomes filled with cells which have been budded from the outer wall of the right posterior cœlom. The posterior pedicellaria is situated just about where the right and left posterior cœloms abut on one another, and it is in later stages a useful mark for orientation. Figs. 39*a* and 39*b*, taken from two older larvæ, show two later stages in the development of the pedicellaria. The end of the knob becomes trilobed, and some of the contained cells (*musc.*, fig. 39*a*) become developed into muscle fibres, others forming connective tissue and calciferous tissue. This is one of the few cases where the direct transformation of amœbocytes into muscular tissue has been observed.

At the same time the cells of both posterior cœlomic sacs, right and left, develop transverse muscle fibres at about the level of the posterior epaulettes (*musc.*, fig. 38*b*). These fibres serve to contract the hinder end of the larva, and thus draw together the lower proximal ends of the calcareous rods which support the "arms" of the echinopluteus, and in consequence cause the upper distal ends of these arms to diverge. In the living larva these movements of the arms can be easily observed, and are mentioned by Théel (26). Both right and left sacs have now spread so far in a dorsal-ventral direction that they occupy the whole side of the stomach, as well as extending to the posterior pole of the larva.

When the larva has attained an age of about 33 days, the first traces of the spines of the adult can be traced in the Echinus-rudiment. There are three of these in each interradius, and they are more or less conical in shape (compare fig. 8, Plate 8). They originate as ectodermal outgrowths, the interior of which becomes filled with wandering cells which, uniting with one another, give rise to the calciferous tissue. At first, of course, they are completely contained in the amniotic cavity. By this time the left posterior cœlom is decidedly larger than the right in volume, and it exhibits a tendency to displace the posterior pole of the larva as marked by the pedicellaria to the right side. Both right and left posterior cœlomic cavities have by this time extended quite to the anus, as is shown by fig. 14, Plate 14, and each occupies the whole side of the larva from the dorsal to ventral edge, as is shown in fig. 45, Plate 13. At the posterior pole for a considerable distance the mesentery which originally separated them has become absorbed, and they open freely into one another; in front, however, where they abut on the left anterior cœlom or "ampulla," and on the right hydrocœle or "madreporic" vesicle, they remain distinct (fig. 48, Plate 14).

At a period ranging from 36 to 40 days from fertilisation still further changes occur. The echinus-rudiment has by this time become so large that it occupies the entire side of the larva, and at the same time the hydrocœle has become so distended

with fluid as to form a very prominent structure indeed, and to cause the left side of the stomach to be sensibly flattened (compare fig. 49*b*). The dental sacs and their contained teeth are greatly enlarged, and at the same time they have begun to give off narrow diverticula which, insinuating themselves between the hydrocœle and the ectoderm, form the rudiments of the radial perihæmal canals of the adult (*perih.*, fig. 45, Plate 13). The suckers of the tube-feet exhibit in the centre sense-organs consisting of elongated ectoderm cells (*sens.*, fig. 49*b*, Plate 14). In the centre of the ectoderm covering the hydrocœle, that is, on the floor of the epineural space, an invagination makes its appearance (*ad. stom.*, fig. 49*b*) which forces its way through the narrow perforation in the centre of the swollen hydrocœle. This is the rudiment of the œsophagus of the adult, and by the time it appears a hole has been made in the roof of the amniotic cavity (see fig. 45, Plate 13) which gradually enlarges. At the same time the first traces of the dorsal spines of the adult make their appearance on the right side of the larva (*d. sp.* figs. 49*a* and 49*c*, Plate 14); these differ from the ventral spines in having clavate ends of square outline.

At about this time also the so-called blood-system makes its appearance. Throughout the whole development, as can be seen from the figures, the inner wall of the cœlom has never been in immediate contact with the endodermic cells of the œsophagus, stomach, and intestine. Always there has intervened a layer of jelly (*sang.*, figs. 49*a*, *b*, &c., Plate 14), which, in the stage under discussion, alters its chemical characters, as is evident from its acquiring staining properties. As at the same time the cells of the gut become more difficult to stain, it seems pretty clear that the alteration referred to is due to the exudation of some substance, probably of a proteid

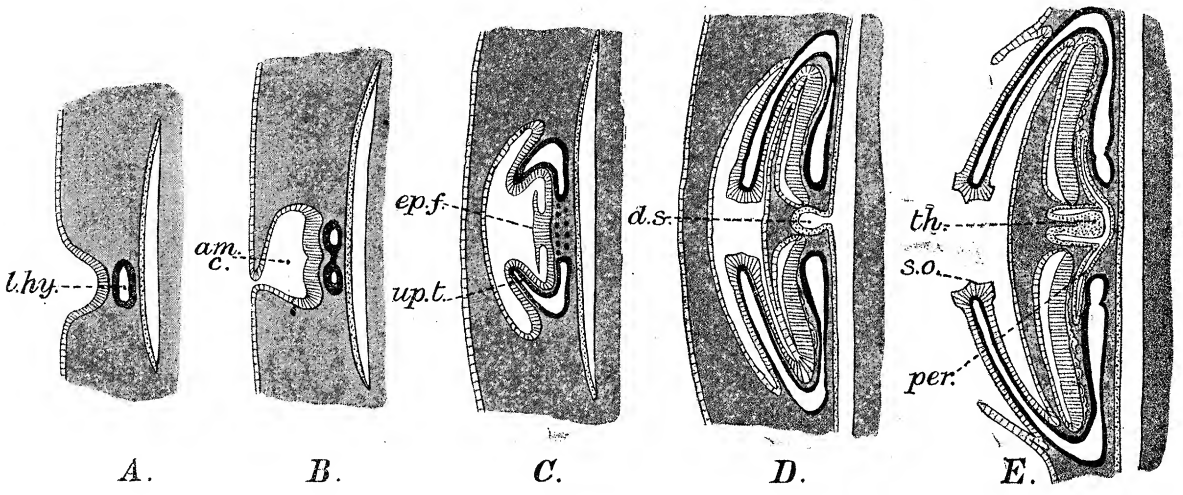

Fig. 5.—Five diagrams to show the gradual growth and differentiation of the echinus-rudiment. *am. c.* amniotic cavity; *d. s.*, dental sac; *ep. f.*, epineural fold; *l. hy.*, left hydrocœle; *per.*, rudiment of the perihæmal canal of the adult; *s. o.*, sense organ on apex of tube-foot; *th.*, rudiment of tooth; *up. t.*, unpaired tube-foot.

nature, from the endoderm cells. Few or no fibres traverse the altered jelly, and the amœbocytes contained in it appear glassy and clear in contrast to the heavily stained medium around them. From this envelope of jelly the mesenteric and the antimesenteric vessels of the adult are developed. All these observations bear out the conclusions I arrived at in my paper on *Asterina gibbosa* (15), that the blood-vessels of the Echinoidea are lymph channels devoid of proper wall and without any circulation of contents, in which the products of digestion accumulate, and possibly from here their most important constituents pass, either by diffusion or the action of amœbocytes, into the cœlomic fluid.

The Metamorphosis.

The change from the larval to the adult condition is comparatively rapid, and is initiated by a gradual reduction of the processes of the ciliated band. This impairs the swimming capacity of the larva, now grown heavy on account of the large size of the echinus-rudiment and the calcareous matter of the spines developed on it; as a consequence the larva sinks lower and lower in the water, and is found near the bottom. It is comparatively difficult to secure specimens in the act, so to speak, of transition; by assiduous search, however, I secured several, of which one, an echinopluteus of *Echinus miliaris*, is represented in Plate 8, fig. 8; and from another, an echinopluteus of *Echinus esculentus*, the sections represented in figs. 49*a*, *b*, and *c*, Plate 14, are taken. The latter when I captured it was actually creeping on the bottom by means of its primary tube-feet, whilst the ciliated epaulettes remained quite distinct though somewhat shrunken, and most of the "arms" were also visible. In Plate 8, figs. 7 and 8, it can be seen that in *Echinus miliaris* the "Echinus-rudiment" is situated in the re-entrant angle of the ciliated band between the post-oral and postero-dorsal arms, and that as the rudiment enlarges this re-entrant angle becomes pulled out, and its apex, along with the posterior pole of the larva, pushed over to the right side. It can be further seen that the first part of the ciliated band to disappear is the post-oral arm of the left side, quickly followed by the left postero-dorsal arm. In the larva of *Echinus esculentus* there disappears, in addition, a large portion of the anterior epaulettes which have extended on to the roof of the amniotic cavity. The hole in the roof of the amniotic cavity has by this time extended so much that all the five tube-feet can be freely extended; indeed, all that is left of the roof is a slight fold, the amniotic fold (*am. f.*, figs. 49*a*, *b*, and *c*), round the edge of the enlarged echinus-rudiment, or as we may henceforward call it the oral disc of the sea-urchin. In *Echinus miliaris* each primary tube-foot has already given rise to a pair of lateral tube-feet (*pod.*, fig. 8, Plate 8), but that is not the case with *Echinus esculentus*. The ventral spines show conspicuously the differentiation into spine in the narrow sense, and boss with which the free spine articulates, and round the base of the former is an ectodermic thickening which will give rise to the

nerve ring round the base of the adult spine. These spines are evidently already organs of locomotion. The larval œsophagus still communicates with the stomach, but it is very much contracted just below the inner end of the adoral ciliated band, and its outer portion exhibits a tendency to become everted and flattened out, as is seen by the way in which the adoral band is exposed (*cil. ad.*, fig. 8, Plate 8). The larval anus has already become closed (fig. 49*c*, Plate 14).

By this time also the rudiment of that curious organ which was formerly called the "heart," but which in *Asterina gibbosa* I showed to be the first rudiment of the genital system, has made its appearance (*gen. st.*, fig. 50, Plate 14). In *Echinus esculentus*, just as in *Asterina gibbosa*, it originates from the wall of the left posterior cœlom, close to the septum separating it from the left anterior cœlom. In Asterina it is at first hollow, but in Echinus it is from the first a solid outgrowth of cells.

Once the larva has sunk to the bottom it rapidly loses all appearance of an echinopluteus. The absorption of the ciliated band arms and epaulettes already begun is rapidly carried to completion. The ectoderm of the epaulettes is invaginated and then apparently devoured by large pigment-bearing amœbocytes (*pig.*, fig. 51, Plate 15, and fig. 55, Plate 14). At least these cells which bear granules of a darkish green pigment are seen surrounding the patches of invaginated epithelium and actually inside them. It is true that at an earlier period of development it was shown the cells bearing the red larval pigment were excretory in function, and the same may be true of these cells, in which case they probably fill both functions. The ectoderm cells covering the arms shrink, leaving the calcareous rods exposed (*pl. sp.*, fig. 11, Plate 8), exactly as happens in the case of unhealthy larvæ in all stages of development. The outer part of the larval œsophagus becomes completely separated from the inner part and then shallows out and disappears, and with it goes the whole of the oral lobe of the larva, including the whole of the right anterior cœlom and the front portion of the left anterior cœlom, and the animal is deprived of all appearance of an echinopluteus, and assumes an almost hemispherical form with a flattened ventral and a humped dorsal surface (fig. 11, Plate 8, and fig. 55, Plate 15). The inner part of the larval œsophagus persists for some time as a completely closed tube lined by pale degenerating cells (*l. œs.*, fig. 55).

During this time the stomach has been undergoing that extraordinary change called *histolysis*. Up to the time of the metamorphosis it was tensely filled with fluid (see fig. 34, Plate 12), and its wall consisted of a single layer of cubical cells, as is well shown in fig. 46, Plate 13. It now loses its turgidity altogether, and its wall becomes much thicker and thrown into numerous folds. In some specimens at this stage the lumen almost entirely disappears. At the same time the cells composing the wall multiply with great rapidity, and round themselves off (see fig. 51, Plate 15, and fig. 55, Plate 16); large numbers migrate into the surrounding jelly, whilst from the residue the epithelium is reconstituted. The intestine is already distinguishable from the stomach by the lesser capacity of its cells for stain; a distinction which remains

throughout life; it does not usually undergo histolysis at all (note fig. 55, Plate 16).

The hydrocœle loses a great deal of the turgidity which it possessed just before metamorphosis, and it is now perforated by the adult stomodæum (*ad. stom.*, fig. 53, Plate 15). At the same time a solid outgrowth of cells has made its appearance in the centre of the ventral (larval left) wall of the stomach (*ad. œs.*, fig. 53, Plate 15). This is the rudiment of the endodermal portion of the adult œsophagus, and it meets the adult stomodæum at a later stage.

Calcification has begun in the jaws and the teeth. This is well seen in fig. 10, Plate 8, where in each interradius three calcareous pieces can be seen shimmering through the epineural veil which still covers the opening of the adult stomodæum. The centre one of each group is the tooth, the two lateral are the alveoli, which subsequently by their union form the jaw. In the section represented in fig. 53, Plate 15, the evidence of calcification is seen in the spaces marked *calc.*, which appear at the midst of the cellular rudiment of the tooth. These spaces were occupied in the living animal by calcareous matter, which has been removed in the process of preservation.*

We see then that immediately after metamorphosis the young *Echinus esculentus* is devoid of both mouth and anus. It has a convex dorsal surface bearing clavate spines, and three pedicellariæ (fig. 11, Plate 8), which is quite equal in extent to the ventral ambulatory surface. It walks by means of five tube-feet, each forming the termination of one of the radial canals, and each provided with a sucker, in the centre of the disc of which is a sense-organ consisting of elongated cells. The rudiments of a pair of tube-feet are present in each radius (*pod.*, fig. 10, Plate 8), but they are not functional; in the corresponding stage, however, of *E. miliaris* they are actively functional. In each interradius there are three conical spines which are movable and provided with a nerve collar round the base, so that they can assist in locomotion.

The Further Growth of the Young Sea-urchin.

The material on which this section of my work was based consisted chiefly of a collection of extremely small urchins, from a half to three-quarters of a millimetre in diameter, which I dredged up in Plymouth Sound, just as the larvæ were completing their development in the culture jars. I cannot definitely assert that they

* THÉEL (footnote, p. 301) doubts the accuracy of this statement, but I have traced the tooth-rudiment from the stage where it consists of a single layer of cells forming part of the wall of the dental sac, through the stage when it is many-layered till the cavities showing the presence of calcification make their appearance. In general, as THÉEL remarks, the calcareous skeleton of Echinoidea arises from amœbocytes, but as these were budded from the cœlomic wall, the difference between the two cases is not so great as he supposes.—*November* 6, 1902.

are *Echinus esculentus*; they may be *Echinus miliaris*, but the development of these two species does not differ sufficiently to make this a matter of much importance. In addition to this collection, between the youngest of which and the oldest of the artificially reared specimens there was no great gap, I made use of another collection of older specimens dredged in the Bay of Naples in 1892, and probably belonging to one or more of the common Neapolitan species, *E. microtuberculatus*, *Sphærechinus granularis* and *Strongylocentrotus lividus*. One of the most interesting features in the further development of the young sea-urchin is the gradual extension of the ventral ambulatory surface, and the diminution in size of the unpaired tube-foot in each radius, its place being taken by the paired tube-feet, of which there are more and more successfully developed. If fig. 52, which represents a section through a specimen about ·7 millim. in diameter, be compared with fig. 51, representing a section of a specimen which has just completed its metamorphosis, these points will be clearly seen. In fig. 52 the radial canal of the water-vascular system and the underlying radial nerve are strongly bent upwards, and the unpaired tube-foot has lost its sucker and become converted into a rounded nodule. It is clearly seen that the whole arched dorsal surface of the just metamorphosed sea-urchin will be converted into the periproct of the adult; at this stage the periproct is still very large, and we might with justice say that the young Echinus was passing through a Cidaris stage. A little later the terminal tube-foot becomes surrounded by an upgrowth of the test to which it becomes adherent (*t.*, fig. 54, Plate 15).

It has now attained the condition which it retains throughout life, viz., that of a nodule, which hardly perceptibly projects above the general level of the test. It is called the "eye" because it is pigmented, and because it is undoubtedly homologous to the unpaired ocular tentacle at the tip of the arm of an asterid; but it is very doubtful if it has really visual functions. At any rate, the brothers Sarasin (21) have shown that in a Cingalese species of Diadema, which is strongly sensitive to light, the visual organs are scattered all over the test and have quite a different structure from that of the so-called eye, which even in this species remains quite insignificant.

Before the urchin acquires a diameter of half a millimetre the adult stomodæum meets the outgrowth from the stomach, and thus a functional mouth and œsophagus are established; the epineural veil becoming at the same time absorbed in the centre, and remaining only at the sides as a covering for the circular epineural canal underlying the nerve-ring.

The perihæmal spaces become completely separated from the dental sacs, and the latter become greatly enlarged and distended with fluid, whilst from their walls the muscles moving the whole apparatus are developed (*musc. exp.*, *musc. cp.*, fig. 54). If at the same time one traces in a series of sections the dental sacs downwards towards the mouth, one finds that each divides into two, which are already commencing to project slightly at the sides of the mouth, and are the rudiments of a pair

of gills. The turgidity of these dental sacs is evidently correlated with their assumption of the function of reservoirs for the fluid contained in the gills, in and

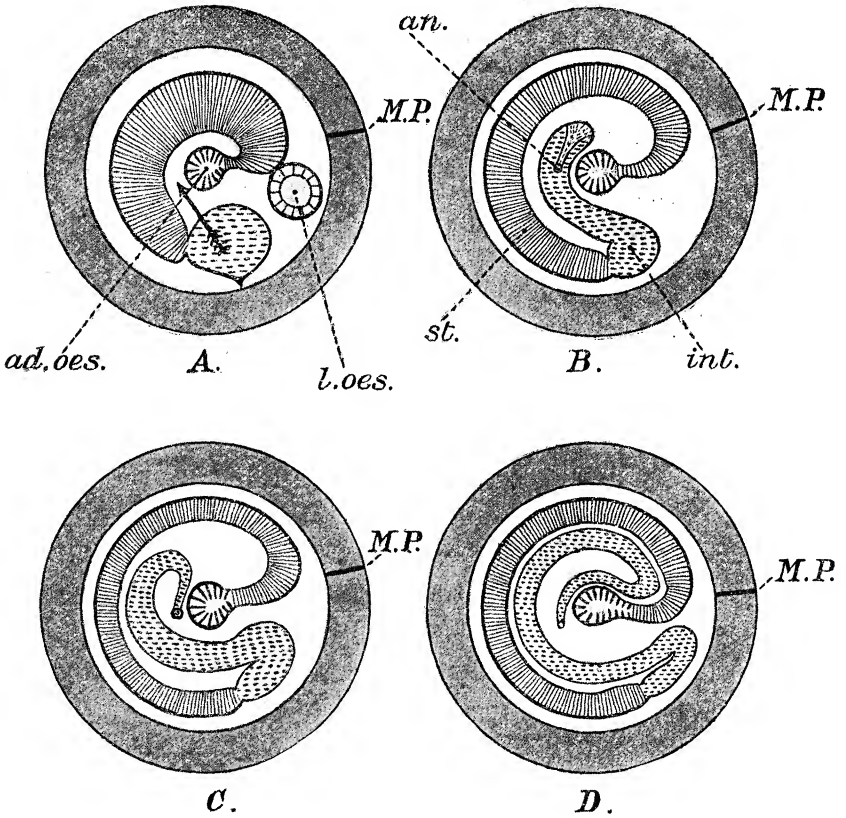

Fig. 6.—Four diagrams showing the manner in which the larval gut is transferred into the adult alimentary canal; *ad. œs.*, adult œsophagus; *l. œs.*, larval œsophagus; *an.*, annas; *int.*, intestine; *st.*, stomach; M.P., interradius in which the madreporite is situated. The arrow in diagram A shows the direction in which the anus migrates.

out of which the water is pumped by the muscles termed the elevators and depressors of the radii, as shown by VON UEXKÜLL (27).

The adult anus is slower in making its appearance than the adult mouth. No trace of it can be seen before the sea-urchin has attained a diameter of 6 millims. The alimentary canal still more slowly attains its adult form. As is well known this structure in the group Echinoidea consists of two coils in opposite directions, the upper one leading to the anus being known as the recurrent coil. By a careful examination and comparison of sections parallel to the disc going back to the stages before metamorphosis, it can be established that the first coil of the alimentary canal is simply the slightly altered flexure of the larval gut, as shown in fig. 34, Plate 11, and text-fig. 6A. This is shown by the position of the persistent vestige of the larval œsophagus in the just metamorphosed specimen (see fig. 55*a*, Plate 16). As compared with the larva the chief change to be noted is that the globular

stomach has become concave on one side. The recurrent coil does not make its appearance till after the anus is formed, and is not complete till the urchin has acquired a diameter of 2 or 3 millims. It is caused by the gradual lengthening of the intestine, the anus and the point of union with the stomach being fixed points (see text-fig. 6, B, C, and D). The cells forming the wall of the stomach and that of the intestine are similar in shape, but, as has already been mentioned, they differ in their reactions to staining material, those of the stomach colouring much browner with osmic acid than those of the intestine.

It remains to speak of the further development of the genital cells. These, as we have seen, first appear as the rudiment of the genital stolon on the larva at the time of metamorphosis. This rudiment consists of a solid cord of cells growing into the jelly from the inner wall of the left posterior cœlom (fig. 50, Plate 14). This cord extends inwards towards the concavity of right hydrocœle, which has now assumed a crescentic form (*r. hy.*, fig. 56), and from this point it also extends along the side of the stone-canal towards the hydrocœle, an extension of the left anterior cœlom or ampulla accompanying it in its growth (*l.a.c.*, fig. 56). At the same time it gives rise to a lateral bud of larger cells (*gen. r.*, fig. 57), which is already conspicuous in an urchin having a diameter of 7 millims. This is the rudiment of the genital rachis, the circular cord of germ cells from which the genital organs later arise as branches. In a specimen having a diameter of about $1\frac{1}{3}$ millims. the genital rachis has commenced to extend in a horizontal direction from the genital stolon, and as it does so it is seen to be enveloped in a fold of the cœlomic wall, which it pushes before it. Between this fold and the rachis there is a narrow extension of the cœlomic cavity (*ab.*, figs. 57 and 58, Plate 16), at first in open communication with the rest, but soon becomes completely closed off. This is the aboral sinus, which thus is seen to have a precisely similar origin to the similarly named organ in *Asterina gibbosa*. When the urchin has attained the diameter of about 3 millims. the genital organs commence to appear as branches from the rachis.

The genital stolon when fully developed has the structure shown in fig. 59, Plate 16. The frame work of the organ consists of a mass of connective tissue, interspersed amongst the fibres of which are the characteristic cells which have been derived from a downgrowth of the genital rudiment seen in the metamorphosing larva. On the outer side the organ is covered by a row of cubical cells forming the wall of the extension of the "ampulla" which adjoins it. An extension of the right hydrocœle adjoins it on the other side, but as we trace the organ in a series of sections towards the water-vascular ring, this dies out, and at the same time the tissue of the stolon more and more surrounds the extension of the ampulla, till this appears as a small space in the centre of a mass of tissue. The Sarasins (22), misled by this appearance, considered the extension of the "ampulla" as a tube with glandular walls, and suggested that it was an excretory organ or "kidney" (Niere), The right hydrocœle they named "Nebenniere" (accessory kidney).

CUÉNOT, who was the first to assert that the genital stolon was the structure from which the rachis took its origin (6), in a later paper recalls this statement, and asserts that genital rachis and genital stolon are totally independent structures (7). In my paper on *Asterina gibbosa* (15) I traced every step in the formation of the rachis and the stolon, and showed that they both sprang from a common rudiment, and I have only to add that the development of *Echinus esculentus* entirely bears out the conclusions I arrived at in the case of *Asterina gibbosa*.

General Conclusions.

On reviewing the whole course of the development which has just been described, the main question which arises is: What is the relation of the larval history of *Echinus esculentus* to the corresponding stages in the development of *Asterina gibbosa*? The resemblances are in the broad outlines of the development, in the method of formation of the archenteron and the cœlom, in the subsequent metameric segmentation of the cœlom, and the ring-like growth of the left posterior cœlom, and in the method of formation of the perihæmal spaces of the "blood-system" and the genital organs.

The differences, leaving out of sight those features of the larva of Asterina, which like the loss of the ciliated band and the larval intestine, are exceptional amongst the Asteroidea, and result from its shortened development, can be summed up under three heads. As compared with Asterina, the development of Echinus exhibits (1) the entire missing out of certain stages in the development of the larva, (2) the precocious appearance and shortened development of certain organs, (3) the substitution in certain cases of solid outgrowths of cells for evaginations of the wall of hollow organs.

Considering first the resemblances: it will be seen that they entirely confirm the conclusion I arrived at in my paper on *Asterina gibbosa*, that the bilateral free-swimming ancestor of the echinoderms, to whose existence the larvæ point, had a trifid division of the cœlom, and, so far as this organ was concerned, the same structure as the Tornaria larva of Balanoglossus now exhibits; that it further resembled this larva in the course of main ciliated band, and in the possession of an apical plate of neuro-epithelium, and that therefore both Echinodermata and Enteropneusta are descended from a common free-swimming ancestral group, for which I proposed the name Protocœlomata, and to this name I adhere.

Secondly, it is clearly shown that the five dental sacs which together constitute the "lantern cœlom" in Echinus, correspond in development as in position with the so-called outer perihæmal ring of Asterina. This, as I showed in the paper alluded to, is not a ring at all, but consists of five wedge-shaped spaces apposed to one another, extensions of which constitute the radial perihæmal canals. From the walls of these spaces in Asterina are derived the muscles which move the ambulacral

ossicles on one another, and from the walls of the dental sacs in Echinus the muscles which move the jaws. Hence the jaws, since they are interradial in position, may be looked on as corresponding to the adambulacral ossicles of two adjacent rays, whilst the tooth represents the bunch of spines often borne by the projecting mouth-angle in Asteroidea. The great extension in size of the spaces corresponding to the perihæmal ring accounts for the wide separation of the nerve ring from the water-vascular ring, and the appearance of a stomodæum, a feature unknown heretofore in any other *adult* echinoderm.

Turning now to the differences: first, the substitution of solid outgrowths for hollow evaginations in the case of the formation of the right hydrocœle and of the genital stolon, is one of the commonest modifications of development known, and many instances of parallel cases could be selected from almost any group in the animal kingdom. In the case of Echinus we can form a tolerable guess at its proximate cause. The cœlom in the echinopluteus has, compared with that of the larva of Asterina and even of the Bipinnaria larva, an exceedingly narrow lumen. Hence the lumen of outgrowths from it, which even amongst the larvæ of Asteroidea is small, tends to vanish.

Secondly, the missing out of stages in the life-history, as compared with the life-history of Asterina. The stage which is missed out is the fixed stage: the animal passes at a single bound, so to speak, from locomotion by means of cilia to locomotion by means of tube-feet. Is therefore the fixed stage of the Asteroidea to be looked on as a secondarily intercalated stage, a falsification of development, or not? Now in seeking in ontogeny for light on phylogenetic history, we must always regard as primitive any gradual transition from one set of habits to another, and any structure which implies such a transition. The fixed stage in *Asterina gibbosa* is just the link we require to connect the habits of the swimming larva with its præ-oral lobe directed forwards with the vague wanderings of the adult in which any radius may be directed forwards. A fixed habit tends to bring about the development of radial symmetry first in the external organs and later in the internal organs correlated with them, and how the fixed habit was gradually acquired is shown by the earlier larva of Asterina, which swims slowly about by means of its cilia, occasionally attaching itself voluntarily by means of the præ-oral lobe. So we can picture to ourselves the bilateral ancestor at first temporarily attaching itself and using the current produced by its cilia for feeding itself. A permanently fixed echinoderm feeding itself by means of a ciliary current is of course the normal type amongst the Crinoidea. We therefore conclude that the fixed stage has been missed out in the case of Echinus, and not secondarily intercalated in Asterina, and this conclusion will at once account for several of the peculiarities of the echinopluteus; thus the præ-oral lobe, the former organ of fixation, has become greatly reduced in size, and the extensions of the cœlom into it correspondingly small, and they fail to unite into a single anterior cœlom as they do in the Asterid larva.

The primitive type of development, in which the habits and the corresponding organs of one stage pass by slow transitions into those of another, is one which inevitably tends to become modified, since the dangers to which the larva is exposed are multiplied by every mode of life and corresponding environment it passes through on the way to the adult condition, in each of which it finds competitors for food. Hence arises the tendency to accumulate in one stage enough food to carry on development over the next without the necessity of feeding. This tendency may manifest itself in two ways: if the food be stored in the egg, as yolk, a part of the development at any rate will be passed in the embryonic condition within the shelter of the egg-shell, and the gradual transition in structure may be retained, but if the nourishment be accumulated during a larval stage, there will be a tendency to have a long larval period, followed by a quick metamorphosis; in other words, to change a g r a d u a l development into a d i s r u p t i v e one. The organs required for the next stage will, where possible, be developed in a sheltered position, since they are functionless till this stage is entered on. Thus the legs of the house-fly are developed on the floor of pockets of invaginated ectoderm, the so-called imaginal discs of the maggot. Viewed in this light, the development of the echinopluteus stamps itself at once as a highly modified one. The retention of the ciliated bands, which are the organs of locomotion and nutrition of the larva, until just before the metamorphosis, is due to the necessity of prolonging the larval habits till those of the adult are ready to be taken up.

The development of the adult organs within the sheltering protection of the amniotic cavity is exactly parallel to the development of the legs and wings of an insect imago from the imaginal disc of the larva. The modified character of the echinopluteus is further shown by the appearance of the left functional hydrocœle from the first as a five-lobed disc, which soon becomes changed into a ring through which the adult œsophagus later grows. This is an instance of what may be termed *dislocation of development*, or the appearance of organs out of their proper order. In the larvæ of Ophiuroidea and Holothuroidea the larval œsophagus becomes directly changed into the adult one, and the hydrocœle appears as an open hoop and grows round it, and this gradual acquisition of radial symmetry, as it is consistent with the constant use of the mouth, is undoubtedly the primitive mode of development.

Having arrived at the conclusion that the larval history of *Echinus esculentus*, though agreeing in its broad outlines with that of *Asterina gibbosa*, is nevertheless a very modified one, the further question remains as to whether the post-larval history throws any light on the relationship of the Echinoidea to the other groups of the Echinodermata. It may I think be answered that it affords strong evidence of their origin from the Asteroidea. In the just metamorphosed sea-urchin the humped dorsal surface is greater in extent than the flat ventral one, and the radial canals extend straight outwards from the water-vascular ring, and end in prominent

terminal tentacles, both of which are asterid features. Further, the adult form is attained by the slow preponderance in growth of the ventral ambulatory surface, the dorsal surface becoming more and more insignificant. That this is a growth of the whole ventral surface and not merely of the radial areas, is shown by the concomitant extension of the area covered by the conical ventral spines, which as we have seen are at first interradial in position. The early covering over of the radial nerve cords by the epineural folds, so as to form the epineural canals, is to be explained as an instance of the dislocation of development above referred to.

In the recent excellent treatise on Echinodermata published under the editorship of Professor LANKESTER as a volume of his 'Zoology' (2), Messrs. BATHER and GREGORY take the view that the Echinoidea are derived directly from an exceedingly primitive type of echinoderm belonging to that heterogeneous group the Cystoidea. They picture to themselves the ancestral sea-urchin as an irregularly plated sac-like animal, with food grooves, and accompanying extensions of the radial water-vascular canals extending outwards from the mouth. The animal is supposed to have been fixed either by means of a short stem or the aboral surface of the disc. It will be seen that the essential point in this view is, that the characteristic globular form and meridional course of the water-vascular canals of an echinid are primitive features, but the post-larval development as we have just seen shows in the clearest manner, that they are secondary modifications.

Another weighty reason for dissenting from the view of Messrs. BATHER and GREGORY is the universal occurrence of highly developed pedicellariæ amongst Echinoidea. Amongst Asteroidea they are by no means universal, and numerous transitional forms are found, showing their origin from spines; in a word, pedicellariæ have been developed amongst the Asteroidea and inherited ready-made, so to speak, by the Echinoidea. We conclude therefore that Echinoidea are descended from Asteroidea, and we may add from Asteroidea with well-developed pedicellariæ, and the change which has occurred may be expressed by saying either that the dorsal surface has greatly diminished in size, or that the asterid arm, which was developed as a support for the long radial canal, has become re-absorbed into the body, forcing the canal to pursue a curved course, The cause of the change may be at any rate plausibly suggested; the typical sea-urchin is pre-eminently a dweller on rocky ground, and the extension of the ambulatory surface in a meridional direction would under these circumstances be a distinct advantage in enabling the urchin to catch hold of a support, either above or below it.

Summary.

The principal conclusions arrived at in this paper are as follows :—

(1.) The blastula of Echinus contains a comparatively thick solution of proteid, which becomes thinner as development advances, but some of which is found in the

blastocœle or primary body-cavity throughout the whole course of development, and eventually forms the jelly-like ground substance of the test of the adult.

(2.) The mesenchyme cells are connected with each other and the wall of the blastula by protoplasmic strings, but besides these no other protoplasmic structures were observed in the blastocœle of the living blastula.

(3.) The adoral ciliated band is formed from both ectodermic and endodermic cells and produces an inwardly directed current, and hence cannot be compared to the endostyle of the Protovertebrata.

(4.) The madreporic pore is at first a structure distinctly belonging to the left side.

(5.) The cœlom undergoes a metameric segmentation into three divisions on each side of the larva, but the segmentation of the left side precedes that of the right.

(6.) The left functional hydrocœle has at first the form of a disc, which is very early converted into a ring, through which the adult œsophagus later grows.

(7.) There is a well-developed larval nervous system in the shape of an apical plate of neuro-epithelium, corresponding in position to the apical plate of the Tornaria larva, but this plate is not recognisable till the larva is 3 weeks old.

(8.) The epineural canals of the adult are derived from invaginations of the ectoderm.

(9.) The lantern-cœlom of the adult is homologous with the outer perihæmal ring of the asterid, and like it is derived from five evaginated pockets of the cœlom of the left side ; the teeth and jaws are developed from the walls of these pockets.

(10.) The blood-system of the adult originates from the envelope of jelly investing the gut. This jelly becomes changed by the infiltration of some substance exuded from the gut cells.

(11.) The genital stolon arises, as in Asteroidea, as an outgrowth of the wall of the left posterior cœlom, and the genital rachis and the genital organs are developed from it.

(12.) The aboral sinus, as in Asteroidea, is developed as an extension of the left posterior cœlom.

(13.) The first coil of the alimentary canal of the sea-urchin is directly derived from the flexure of the larval gut; whilst the second or recurrent coil is slowly developed after the formation of the adult arms by the lengthening of the intestine.

(14.) The sea-urchin immediately after its metamorphosis exhibits many resemblances to an asterid, and these lead to the belief that the Echinoidea are derived from the Asteroidea.

(15.) The general conclusions as to the ancestry of the phylum Echinodermata as a whole, drawn from a study of the development of *Asterina gibbosa*, are confirmed by the development of *Echinus esculentus*, but the development of the echinopluteus as compared with that of the larva of the star-fish is a highly modified one.

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Description of Plates.

Key List of Abbreviations employed.

ab., aboral sinus. *a. cil. ep.*, anterior ciliated epaulette. *ad. œs.*, adult œsophagus. *ad. stom.*, adult stomodæum. *am.*, amniotic cavity. *calc.*, spaces left by the dissolving out of calcareous matter by the fixing fluid. *am. f.*, amniotic fold, the roof of the amniotic cavity. *amp.*, ampulla. *ap.*, apical plate. *arch.*, archenteron. *cil.*, main ciliated band of larva. *cil. ad.*, adoral ciliated band of larva. *cil. ep.*, ciliated epaulette of larva of *Echinus miliaris*. *cœ.*, cœlomic cavity. *d.s.*, dental sac. *d. sp.*, dorsal spine of the young sea-urchin. *ech.*, invagination to form oral surface of adult. *ep.*, epineural cavity. *ep. f.*, epineural fold. *gen. r.*, genital rachis. *gen. st.*, genital stolon. *int.*, intestine. *l.a.c.*, left anterior cœlomic sac. *l.hy.*, left hydrocœle. *l.œs.*, larval œsophagus. *l.p.c.*, left posterior cœlomic sac. *l.'p.'c.'*, anterior horn of left posterior cœlomic sac. *l. stom.*, larval stomodæum. *mes.*, mesenchyme. *m.p.*, primary

madreporic pore. *musc.*, muscular tissue. *musc. exp.*, expiratory muscle, *i.e.*, the depressor of the "compasses." *musc. i.p.*, interpyramidal muscle. *musc. ret.*, retractor muscle of the jaws. *nerv.*, nervous tissue. *nerv. circ.*, nerve ring. *nerv. rad.*, radial nerve cord. *p.c.*, pore canal. *p. cil. ep.*, posterior ciliated epaulette. *ped.*, pedicellaria. *ped.* 1, *ped.* 2, *ped.* 3, the three pedicellariæ of the larva. *perih.*, perihæmal cavity. *pig.*, pigment bearing wandering cells or amœbocytes. *pl. sp.*, remnant of skeleton of larva. *pod.*, podium, one of the paired tube-feet. *r.a.c.*, right anterior cœlomic cavity. *r.hy.*, right hydrocœle, the madreporic vesicle. *r.p.c.*, the right posterior cœlomic cavity. *sang.*, jelly changed into blood plasma. *st.*, stomach. *st.c.*, stone-canal. *t.*, one of the five azygous tube-feet of the just metamorphosed urchin. *v. sp.*, ventral spine of the young sea-urchin. *w.v. rad.*, radial canal of the water vascular system.

PLATE 7.

Figs. 1*a*, 1*b*, 1*c*. Optical sections of the blastulæ of *Echinus esculentus*, *E. acutus*, and *E. miliaris* respectively, magnified 200 diameters. *mes.*, primary mesenchyme cells.

Figs. 2*a*, 2*b*, 2*c*. Optical sections of the gastrulæ of *Echinus esculentus*, *E. acutus*, and *E. miliaris* respectively. Magnification the same as before. *arch.*, archenteron.

Figs. 3*a*, 3*b*, 3*c*. The larvæ of *Echinus esculentus*, *E. acutus*, and *E. miliaris* respectively, at the age of 3 days, viewed from in front. Fig. 3*d* the larva of *E. miliaris* of the same age, viewed from the side. Magnification the same as before. *cœ.*, primary cœlomic vesicle. *l. stom.*, larval stomodæum, not as yet united to the œsophagus.

Fig. 4. Larva of *Echinus esculentus*, about 7 days old, viewed from in front. Magnified 90 diameters.

Fig. 5. Larva of *Echinus esculentus*, about 23 days old, viewed from in front. Magnification as in fig. 4. *a.p.*, apical plate of neuro-epithelial cells. *a. cil. ep.*, the anterior ciliated epaulettes which are first formed. *p. cil. ep.*, the posterior ciliated epaulette just forming. *ech.*, the ectodermic invagination, the floor of which will form the oral disc of the future Echinus.

PLATE 8.

Fig. 6. Side view of a larva of *Echinus miliaris*, about 6 days old. Magnified 90 diameters. *m.p.*, primary madreporic pore.

Fig. 7. Side view of a larva of *Echinus miliaris*, about 22 days old; *cil. ep.*, the ciliated epaulette. *Ech.*, the rudiment of the oral disc of the future urchin. Magnified 90 diameters.

Fig. 8. Side view of a larva of *Echinus miliaris* in the act of metamorphosis: the "arms," *i.e.*, the processes of the main ciliated band, are already shrivelling. Magnification 125 diameters. *t.*, primary unpaired tube-feet of the young urchin. *pod.*,

the paired tube-feet. *v. sp.*, ventral spine. *d. sp.*, quadrate dorsal spine. *nerv. circ.*, nerve ring. *ad. stom.*, adult stomodæum forming beneath the epineural veil.

Fig. 9. Side view of a larva of *Echinus esculentus*, about 27 days old. *ped.* 2, the dorsal pedicellaria. Magnified 90 diameters.

Fig. 10. Ventral view of a just metamorphosed specimen of *Echinus esculentus*. Magnification 90 diameters.

Fig. 11. Dorsal view of a just metamorphosed specimen of *Echinus esculentus*. Magnification 90 diameters. *pl. sp.*, remnant of the skeleton of one of the "arms" of the larva.

PLATE 9.

(All the figures on this plate refer to *Echinus esculentus*.)

Fig. 12. Longitudinal section of a blastula showing the thick network of coagulated proteid in the interior. Magnified 330 diameters. *mes.*, mesenchyme cells, just being formed.

Fig. 13. Longitudinal sagittal section of a gastrula showing the thinner network of coagulated proteid in the primary body-cavity. Magnification as before.

Fig. 14. Horizontal section of a larva $2\frac{1}{2}$ days old, in order to show the formation of the cœlomic sacs. The coagulated proteid of the earlier stages is only represented by a few sparse strings crossing the body-cavity. *cœ.*, the coelomic pouch of the gut. Magnification as before.

Fig. 15. Optical section of a living blastula compressed under the cover-slip. Magnification as before. The mesenchyne cells are seen to be connected with each other and with the walls of the blastula by strings of living material.

Fig. 16. Horizontal section of a larva $3\frac{1}{2}$ days old. The cœlomic vesicles are separated from the gut. The larval stomodæum is in contact with but does not as yet open into the larval œsophagus. Magnification as before.

Fig. 17. Horizontal section of a larva 4 days old. The stomodæum has now joined the œsophagus and the larval alimentary tract is complete. Magnification as before. *cil. ad.*, the adoral ciliated band, seen, by a comparison with fig. 16, to have been formed from both ectoderm and endoderm cells.

Fig. 18. Horizontal section of a larva $3\frac{1}{2}$ days old, in order to show the junction of the stomodæum and œsophagus. Magnification as before.

Fig. 19. Transverse section of a larva 4 days old, to show the formation of the primary madreporic pore. Magnification as before. *cœ.*, left cœlomic sac. *p.c.*, outgrowth of this sac which forms the pore-canal.

Fig. 20. Transverse section of a larva $4\frac{1}{2}$ days old. Magnification as before. The madreporic pore is open, and is seen to be a structure belonging to the left side. *musc.*, transverse muscles of larval œsophagus in course of formation from cells, budded from the cœlomic sacs.

PLATE 10.

(All the figures on this plate refer to *Echinus esculentus.*)

Fig. 21. Horizontal section of a larva 5 days old. Magnification about 200 diameters. *amp.*, ampulla of the stone-canal formed from the left anterior cœlom.

Fig. 22. Horizontal section of a larva about 6 days old. Magnification the same as in foregoing figure. The cœlomic sacs are beginning to extend backwards along the stomach.

Fig. 23. Horizontal section of a larva 8 days old. Magnification as before. The left cœlomic sac is just dividing into anterior and posterior portions.

Fig. 24. Horizontal section of a larva 8 days old, but more advanced in development than that represented in fig. 23. Magnification as before. The division of the left cœlomic sac is complete.

Fig. 25. Horizontal section of a larva 9 days old, showing the formation of the left hydrocœle from the left anterior cœlomic sac. Magnification as before. *l.hy.*, incipient hydrocœle separated from the anterior cœlom only by a constriction.

Fig. 26. Horizontal section of a larva about 11 days old, showing the completely formed left hydrocœle and the ectodermic invagination growing inwards to meet it. Magnification as before. *ech.*, the invagination of the ectoderm, which will form the future oral surface of the sea-urchin.

Fig. 27. Horizontal section of a larva 12 days old, showing the division of the right cœlomic cavity into anterior and posterior portions. Magnification as before. *p.c.*, the pore-canal leading to the primary madreporic pore cut transversely.

Fig. 28. Horizontal section of a larva 21 days old, showing the division of the left hydrocœle into lobes, and the moulding of the ectodermic invagination on these lobes. Magnification as before. *l.'p.'c.'*, the anterior horn of the posterior division of the left cœlomic sac extending in front of the hydrocœle so as ultimately to completely encircle it. *Musc.*, muscular fibrils developed from the walls of the cœlomic sacs in order to move the skeletal rods supporting the "arms."

Fig. 29. Transverse section of a larva 22 days old, through the œsophagus. Magnified 360 diameters. *musc.*, transverse muscular fibres running from the right to the left anterior cœlomic sac, and serving to constrict the œsophagus.

PLATE 11.

Fig. 30. Transverse section of a larva of *Echinus miliaris* about 17 days old. Magnified 360 diameters. The right anterior cœlom is giving off dorsally a nodule of cells which is the rudiment of the madreporic vesicle or right hydrocœle. *st. c.*,

stone canal; *p.c.*, pore canal; *r.hy.*, nodule of cells, the rudiment of the right hydrocœle.

Fig. 31. Transverse section of a larva of *Echinus miliaris* a little older than that represented in fig. 30. Magnification as before. The right hydrocœle is advanced in development, and the opening of the pore canal into the left anterior cœlom is seen.

Fig. 32. Transverse section of the œsophagus and neighbouring structures of a larva of *Echinus miliaris*, still more advanced in development. Magnification as before. The right hydrocœle is completely separated from the right anterior cœlom. *st. c.*, stone canal; *p.c.*, pore canal.

Fg. 33. Transverse section of the œsophagus and neighbouring structures of a larva of *Echinus miliaris*, about 20 days old. Magnification as before. The right hydrocœle has become a hollow vesicle. *pig.*, pigment-bearing wandering cells.

Fig. 34. Median sagittal section of a larva of *Echinus esculentus*, 20 days old. Magnification 200 diameters. *ap.*, first trace of ectodermic thickening, out of which neuro-epithelial apical plate is developed.

Fig. 35. Lateral sagittal section of a larva of *Echinus esculentus*, 19 days old. Magnification as in fig. 34. The formation of lobes on the left hydrocœle is seen. *ech.*, the ectoderm invagination which becomes applied to the hydrocœle cut obliquely. 1, 2, 3, 4, 5, the lobes of the left hydrocœle.

Fig. 36. Horizontal section through the œsophagus and neighbouring structures of a larva of *Echinus esculentus*, 24 days old. Magnification 360 diameters. *nerv.*, the first nerve fibrils formed under the rudimentary apical plate. *musc.*, the transverse muscles of the larval œsophagus cut across.

Fig. 37. Horizontal section through the œsophagus and neighbouring structures of a larva of *Echinus esculentus*, 50 days old, just about to metamorphose. Magnification the same as in fig. 36. The apical plate (*ap.*) has reached the full development, and has a thick mass of nerve fibrils beneath it.

PLATE 12.

Figs. 38*a*, *b*, &c. Three horizontal sections through a larva of *Echinus esculentus*, 26 days old. Magnified 200 diameters. In each of the sections one of three primitive pedicellariæ is seen to be developing as a rounded nodule. In fig. 38*b* the primary outgrowths of the hydrocœle (*t*) are seen projecting into the amniotic space, and the epineural fold has been developed so as to cover the original surface of the oral disc of the future sea-urchin. The left posterior cœlom has completely surrounded the hydrocœle, as is shown by the position of its anterior horn, *l' p' c'*. In fig. 38*c* the right and left posterior cœlomic sacs are seen to come into contact with one another beneath the intestine.

Figs. 39*a* and *b*. Two stages in the development ot a pedicellaria. Magnified 360

diameters. Fig. 39*a* is taken from a larva of *E. esculentus* about 26 days old, fig. 39*b* from one about 30 days old. The muscles, *musc.*, moving the blades are seen to be developed from wandering cells.

Fig. 40. Horizontal section through the hydrocœle and associated structures of a larva of *Echinus miliaris*, about 25 days old. Magnification 360 diameters. *am.*, amniotic space. *ep. f.*, rudimentary epineural fold.

Figs. 41*a* and *b*. Two horizontal sections through the hydrocœle and associated structures of a larva of *Echinus miliaris* slightly more advanced than that represented in fig. 40. Magnification 360 diameters.

Fig. 42. Horizontal section through the hydrocœle and associated structures of a larva of *Echinus esculentus*, 29 days old. Magnification 360 diameters. *d.s.*, invaginations of the epithelium of the left posterior cœlom which form the rudiments of the dental sacs and the teeth.

Fig. 43. Horizontal section through the hydrocœle and associated structures of a larva of *Echinus esculentus*, 30 days old. Magnification 360 diameters. The dental sac is just being separated from the cœlom. The thickening in its outer wall is the first trace of the tooth. *nerv.*, the nervous fibrils of the developing nerve ring of the adult. *musc.*, muscular fibres developing from the cells of the part of the hydrocœle contained in the primary unpaired tube-feet. (*t.*)

PLATE 13.

(All the figures in this plate refer to *Echinus esculentus*.)

Figs. 44*a* and *b*. Two figures of a frontal section through a larva, 29 days old. Fig. 44*a* shows the whole section. Magnified 200 diameters. Fig. 44*b*, the hydrocœle and adjoining structures. Magnified 360 diameters. *musc.*, circular muscles surrounding the hydrocœle and derived from its epithelial cells. *d.s.*, a completely closed dental sac with the rudiment of the tooth projecting into it.

Fig. 45. Transverse section of a larva, 36 days old. Magnified about 140 diameters. *a.m.*, amniotic space now open to the exterior. *perih.*, perihæmal outgrowth of the dental sac (*d.s.*) arching over a lobe of the hydrocœle, *l. hy.*

Fig. 46. Horizontal section through the hydrocœle and associated structures of a larva, 29 days old. Magnified 1000 diameters, in order to show the first trace of the adult nervous system. *nerv.*, the first nervous fibrillæ formed from the ectoderm of the rudiment of the oral disc of the adult. *musc.*, epithelial cells forming part of the wall of the hydrocœle in the first stage of conversion into muscles.

PLATE 14.

(All the figures in this plate refer to *Echinus esculentus*.)

Fig. 47. Horizontal section through a larva, 33 days old, in the region of the anus. Magnified 200 diameters. *p. cil. ep.*, posterior ciliated epaulette. *r.p.c.*, *l.p.c.*, right and left posterior cœlomic sacs respectively, meeting each other beneath the stomach.

Fig. 48. Horizontal section through a larva, 30 days old, in the region of the œsophagus. Magnified 200 diameters. *st. c.*, stone-canal, opening into the left anterior cœlom, the so-called "ampulla" of the stone-canal. *r. hy.*, the right hydrocœle or madreporic vesicle.

Figs. 49*a*, *b*, *c*. Three horizontal sections through a larva about 42 days old, which, whilst still retaining its ciliated bands, was crawling on the bottom by means of its primary tube-feet. Magnification, 200 diameters. Fig. 49*a* is through the region of the larval œsophagus; fig. 49*b* through the region of the adult stomodæum; fig. 49*c* through the vanishing larval anus. *am. f.*, amniotic fold, the remnant of the roof of the amniotic cavity now freely open to the exterior. *d. sp.*, the first blunt clavate spines of the dorsal regions of the adult. *v. sp.*, the pointed spines of the ventral surface of the adult. *sang.*, the modified jelly surrounding the stomach which gives rise to the so-called "blood-vessels" of the adult. *ad. stom.*, the adult stomodæum arising from the floor of the epineural space. *gen. st.*, the first trace of the genital stolon.

Fig. 50. A small portion of the same section as that represented in fig. 49*b*. Magnified 750 diameters. *st. c.*, stone-canal. *gen. st.*, genital stolon.

PLATE 15.

Fig. 51. Transverse section through a young sea-urchin which has just completed its metamorphosis. Magnification 200 diameters. *st.*, stomach, the epithelium of which is rounding itself off into spherical cells and budding off these profusely into the surrounding jelly; this is the process known as histolysis. *l. œs.*, vestige of the fast-disappearing larval œsophagus. *ad. œs.*, first trace of an outgrowth from the stomach which will meet the adult stomodæum (which is not in the plane of the figure), and so complete the adult œsophagus. *pig.*, pigment-bearing amœbocytes engaged in devouring the invaginated pieces of larval ectoderm. *nerv. circ.*, the nerve ring of the adult now formed.

Fig. 52. Transverse section through a young sea-urchin 7 millims. in diameter. Magnification 90 diameters. The terminal tentacle or unpaired primary tube-foot still projects freely, but has been shifted (as compared with the corresponding structure in fig. 51) dorsally owing to the greater growth of the oral surface. *pod.*, the first paired tube-feet now larger than the unpaired one. *w.v. rad.*, the radial water vascular canal. *musc. i.p.*, the interpyramidal muscles of Aristotle's lantern connect-

ing one jaw with the other. *musc. ret.*, the retractor muscles of the jaws. *nerv. rad.*, the radial nerve.

Fig. 53. Section through a young sea-urchin, which has just completed its metamorphosis, taken parallel to the disc. Magnified 360 diameters. *perih.*, rudiment of the perihæmal radial canal, which is seen to be an outgrowth of the tooth sac.

Fig. 54. Section parallel to the disc of a sea-urchin. ·57 millim. in diameter. Magnified 200 diameters. *amp.*, ampulla of one of the paired tube-feet. The perihæmal cavities are now cut off from those of the tooth-sacs.

PLATE 16.

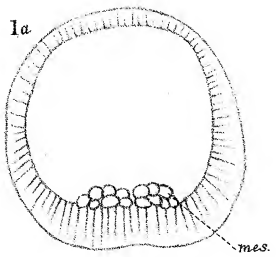
Fig. 55. Section parallel to the disc of a young *Echinus esculentus* which has just completed its metamorphosis. Magnification 360 diameters. The section shows the larval œsophagus and the larval intestine in their relation to the stomach.

Fig. 56. Section parallel to the disc through the genital stolon and adjoining structures in a young sea-urchin 65 millims. in diameter. Magnification 720 diameters. The outline of the pore-canal (*p.c.*) leading from the still single madreporic pore (*m.p.*) to the left anterior cœlom or ampulla of the stone-canal (*l.a.c.*) does not lie completely in the plane of the figure and is consequently dotted for part of its course. *gen. r.*, rudiment of the genital rachis.

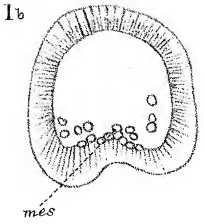
Fig. 57. Section parallel to the disc through the genital stolon and adjoining structures of a young sea-urchin (probably *Echinus microtuberculatus*) 1·28 millims. in diameter. Magnification 360 diameters. *ab.*, first trace of the aboral sinus, an extension of the cœlom surrounding the genital rachis.

Fig. 58. Section parallel to the disc through the genital stolon and adjoining structures of a young sea-urchin (*sp.*) 6·5 millims. in diameter. Magnification 200 diameters. The genital rachis is (*gen. r.*) completely formed, and is enveloped in the aboral sinus (*ab.*).

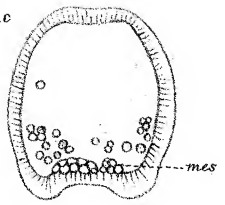
Fig. 59. Another section parallel to the disc of the same specimen as that represented in fig. 58, through the stone-canal and genital stolon. Magnification 360 diameters.



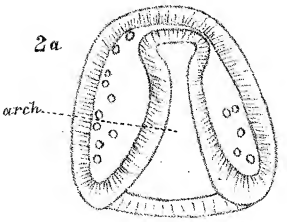
Esculentus



Acutus



Miliaris



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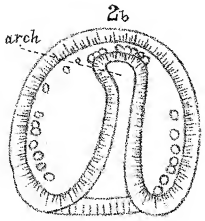

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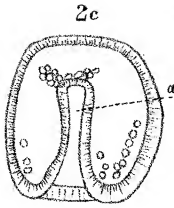

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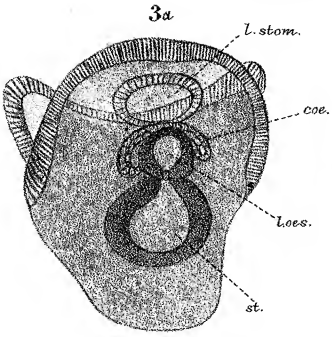

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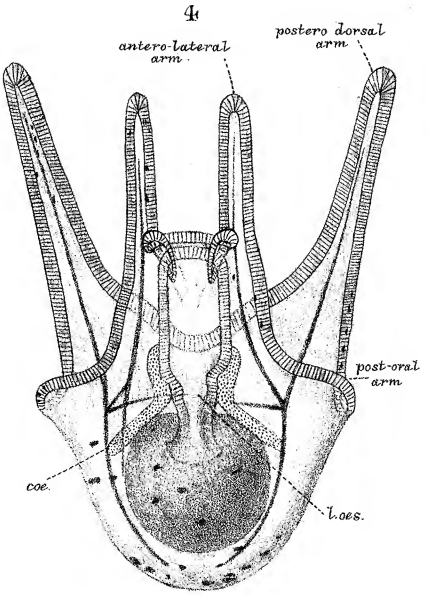

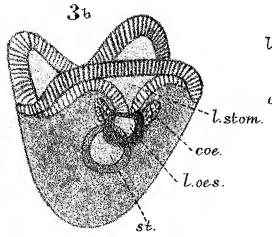

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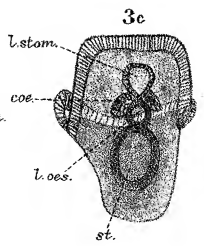

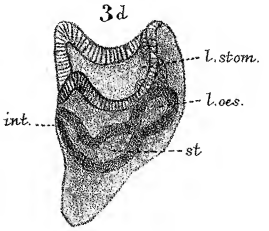

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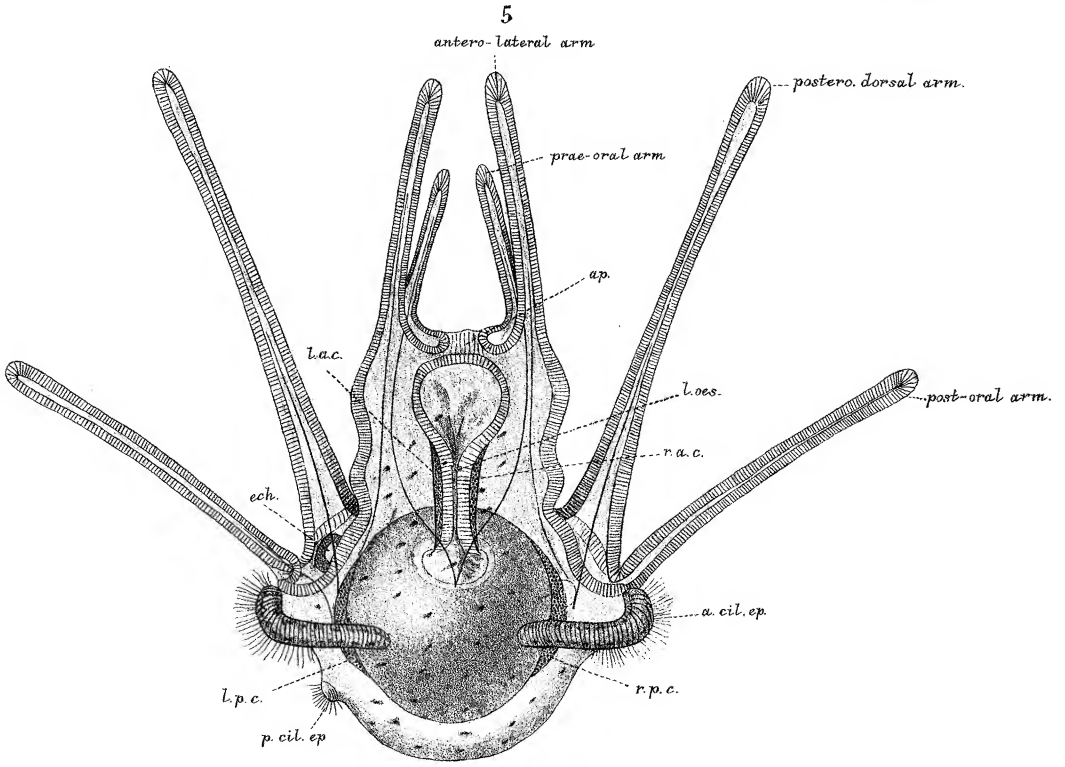
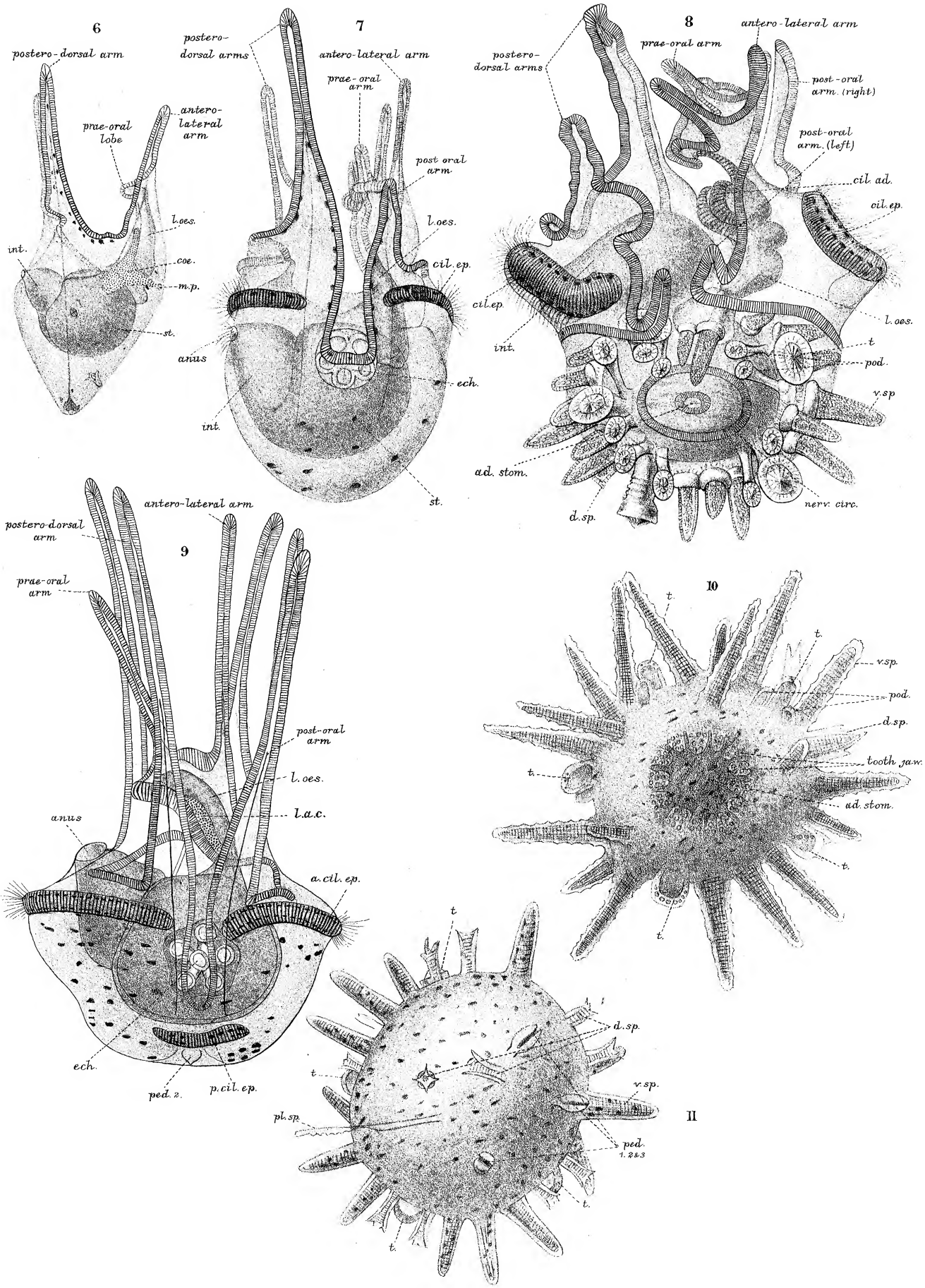
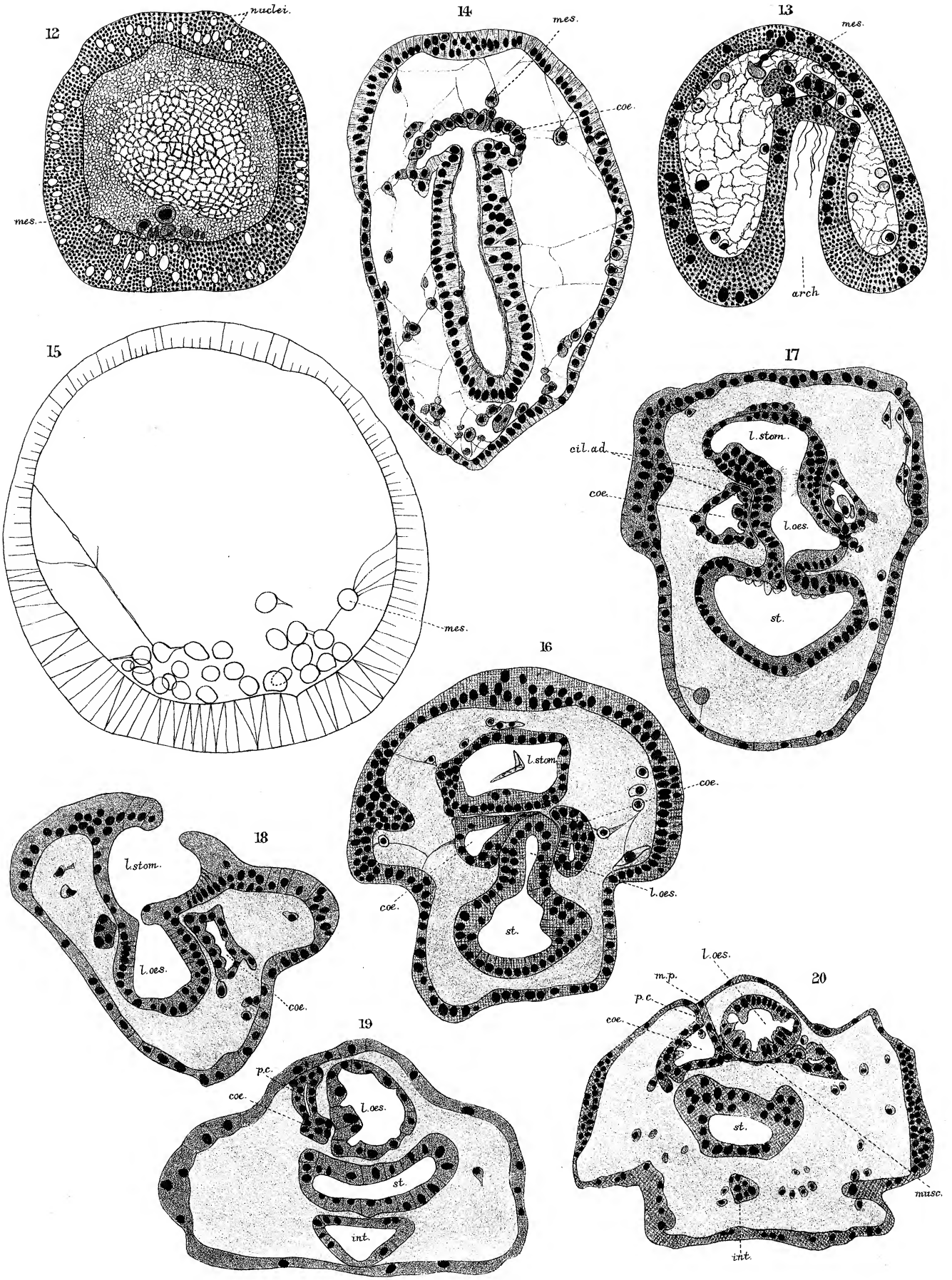




M.P. Parker lith.

Parker & West imp.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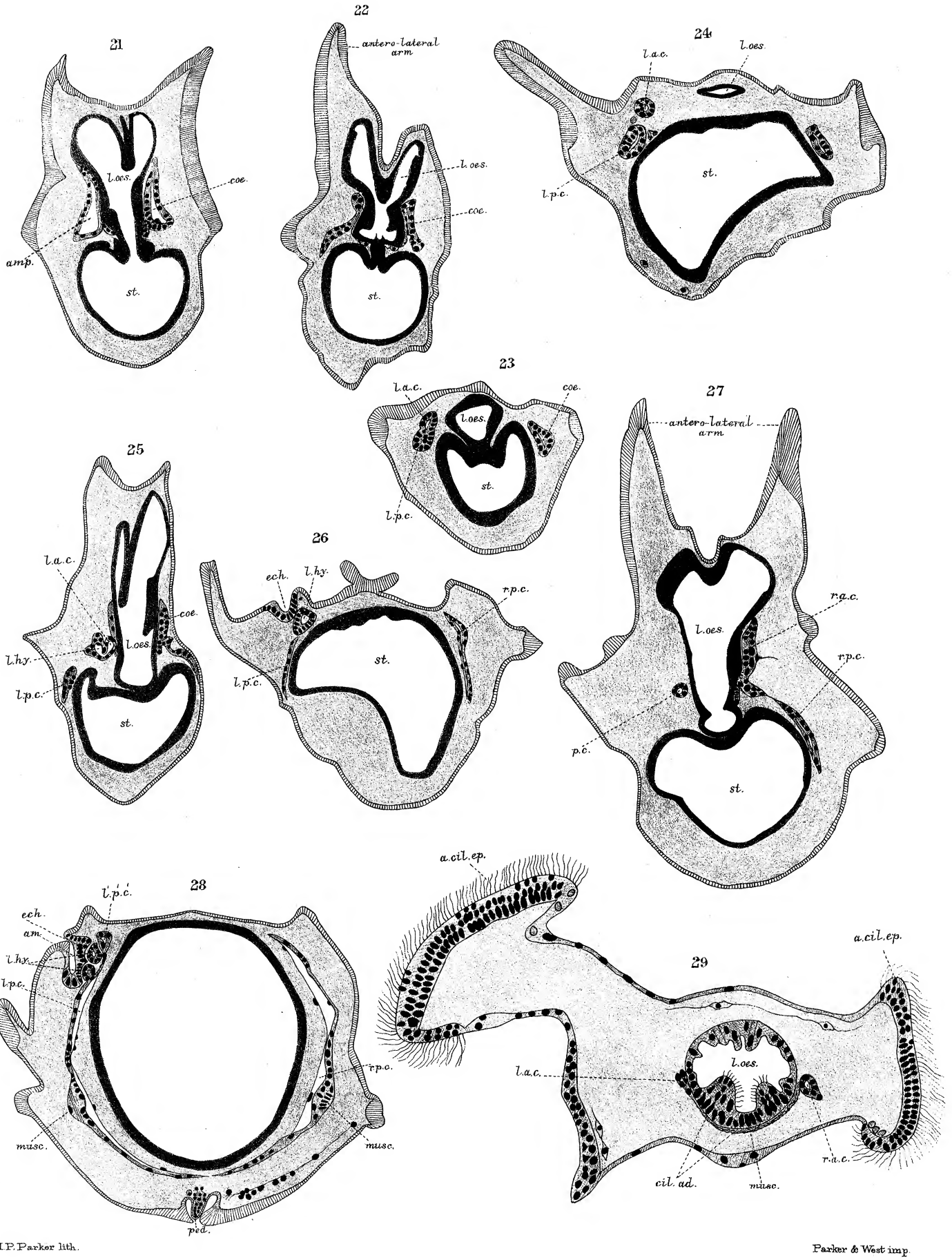

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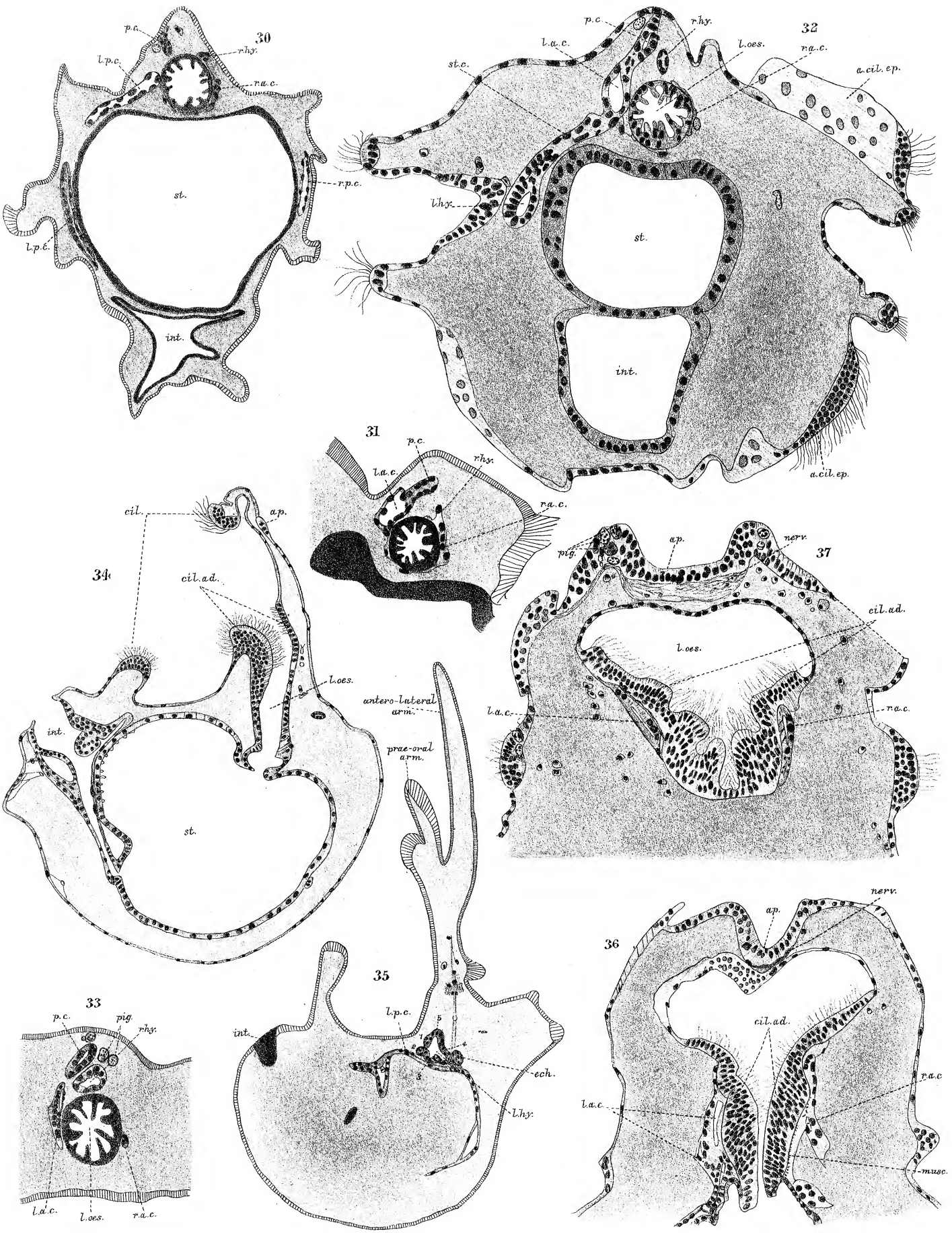

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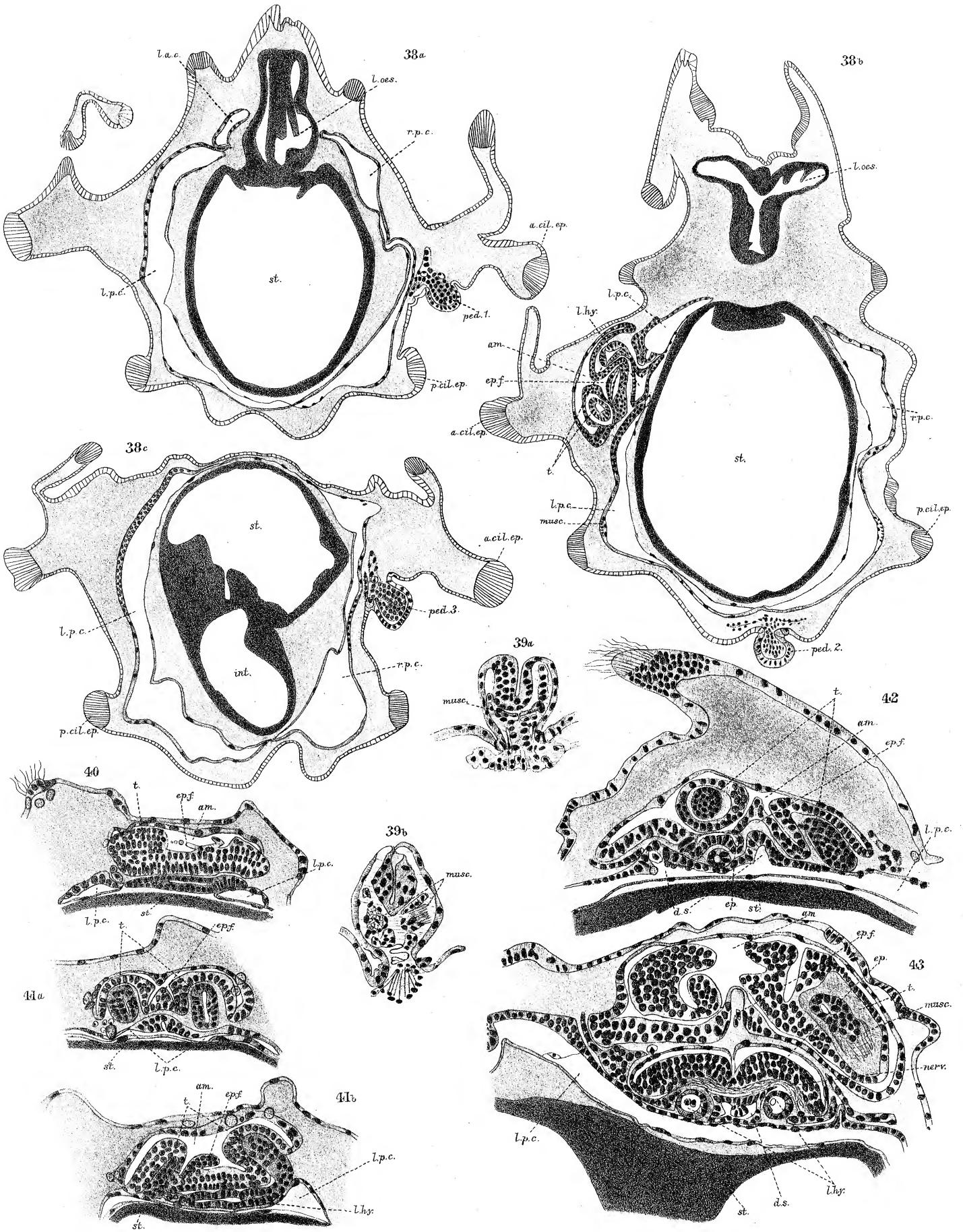
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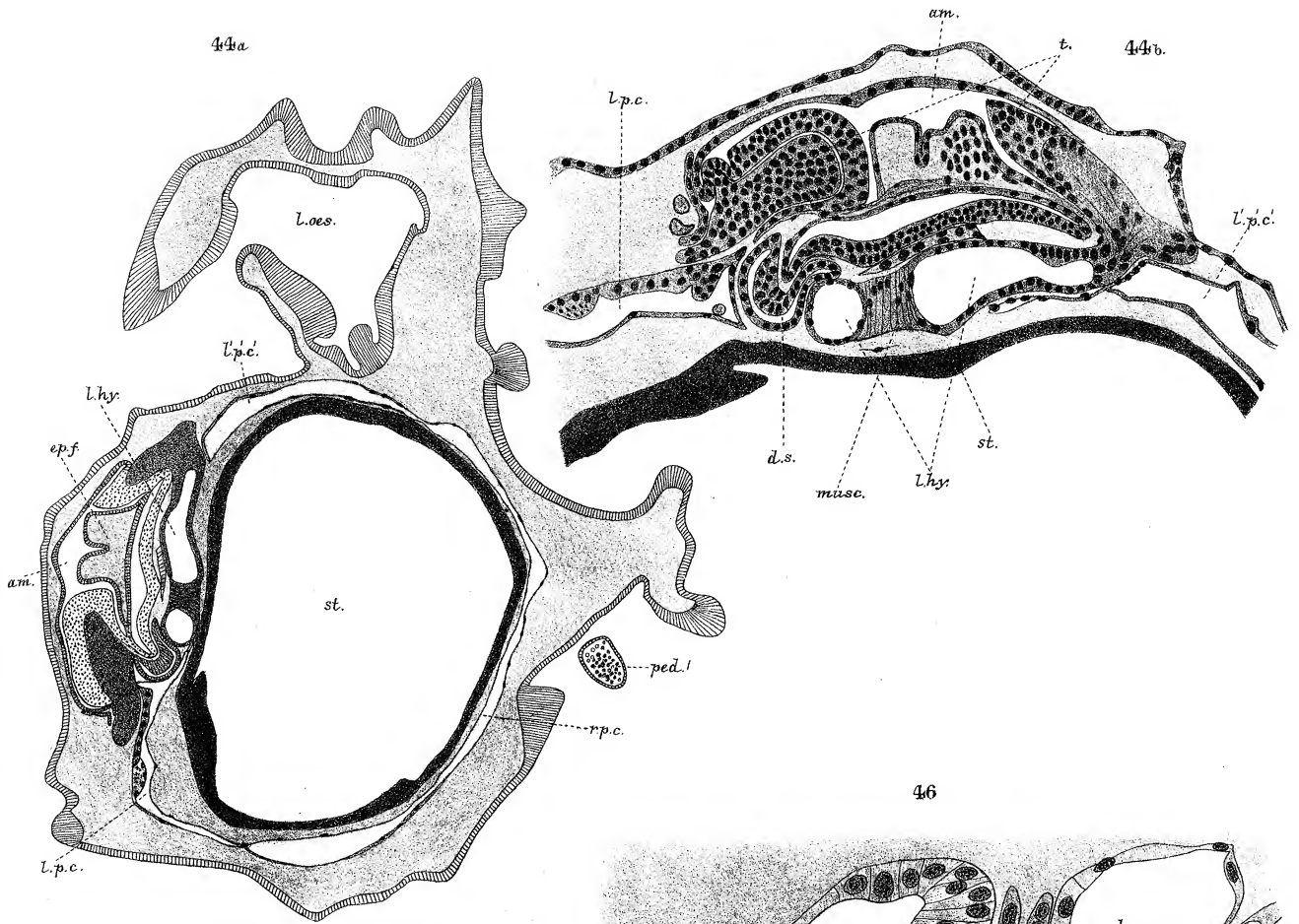
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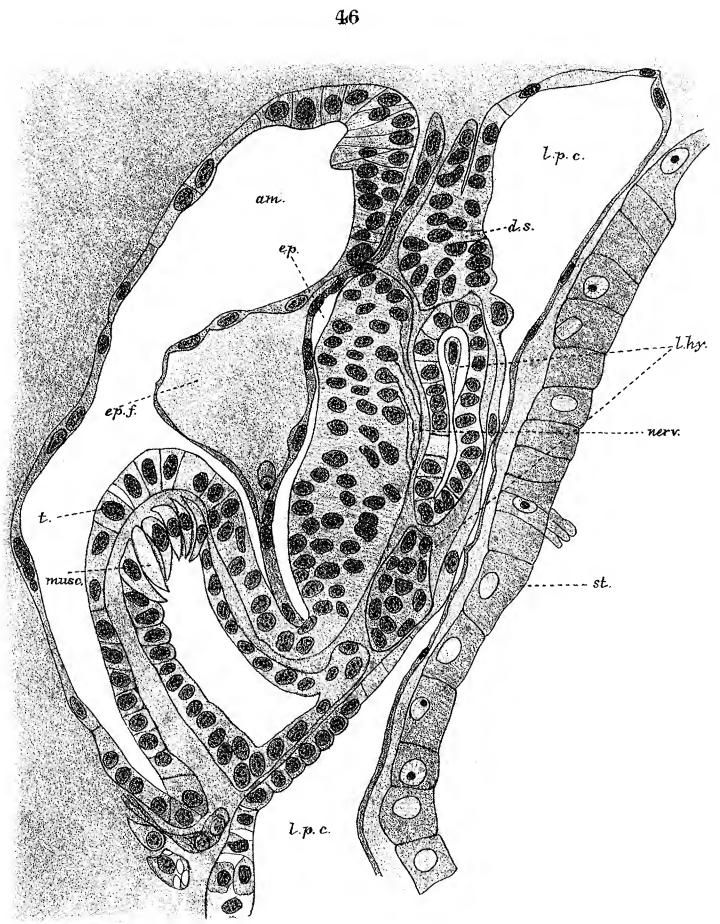
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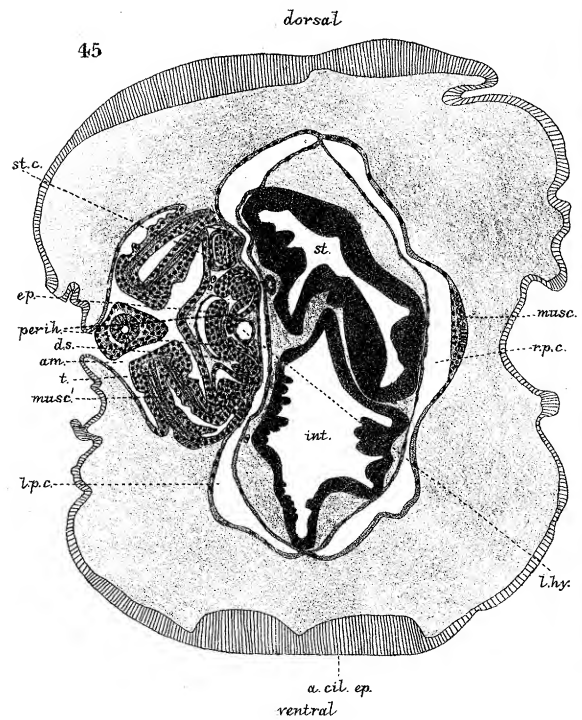
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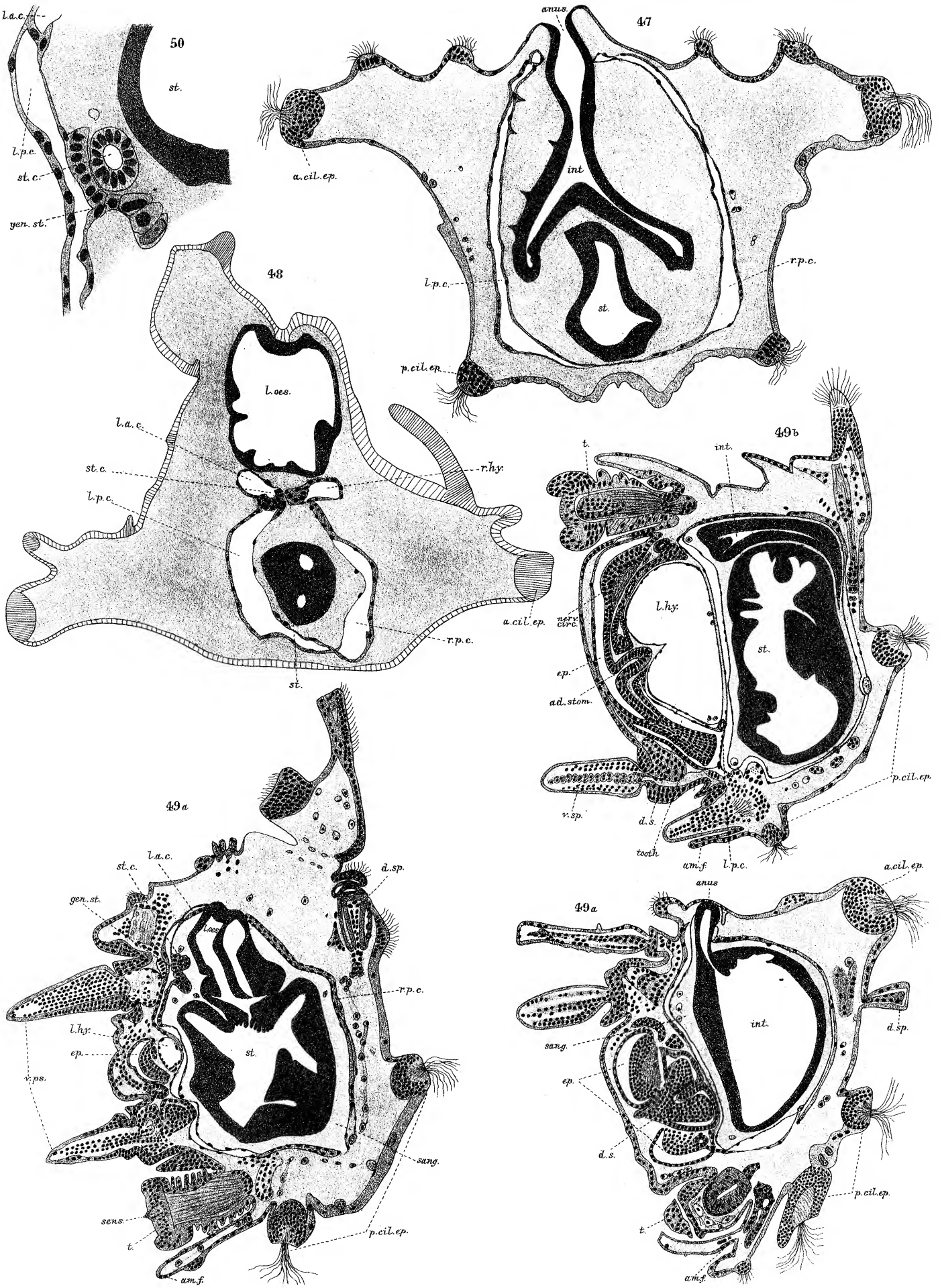
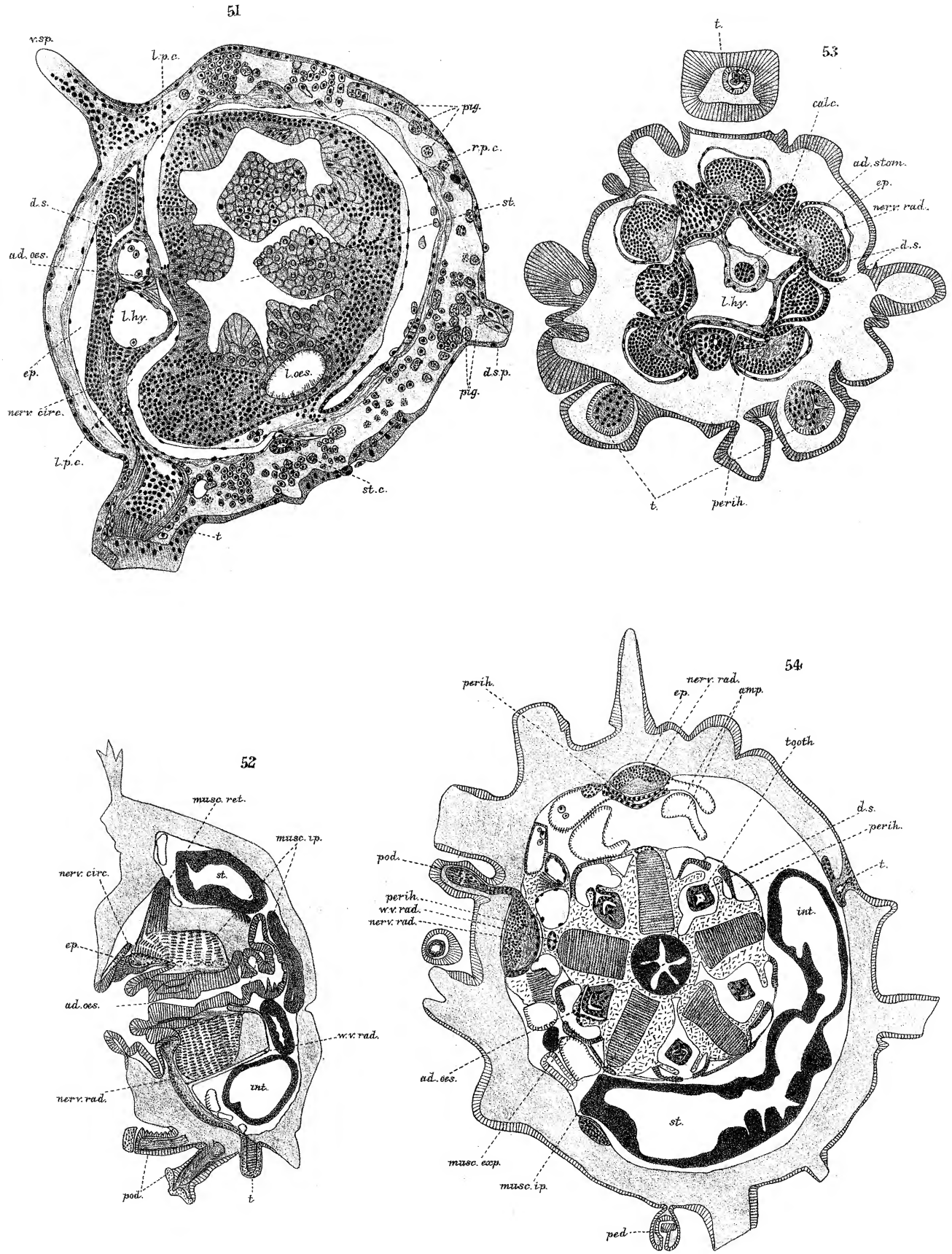


M.P. Parker lith.

Parker & West imp.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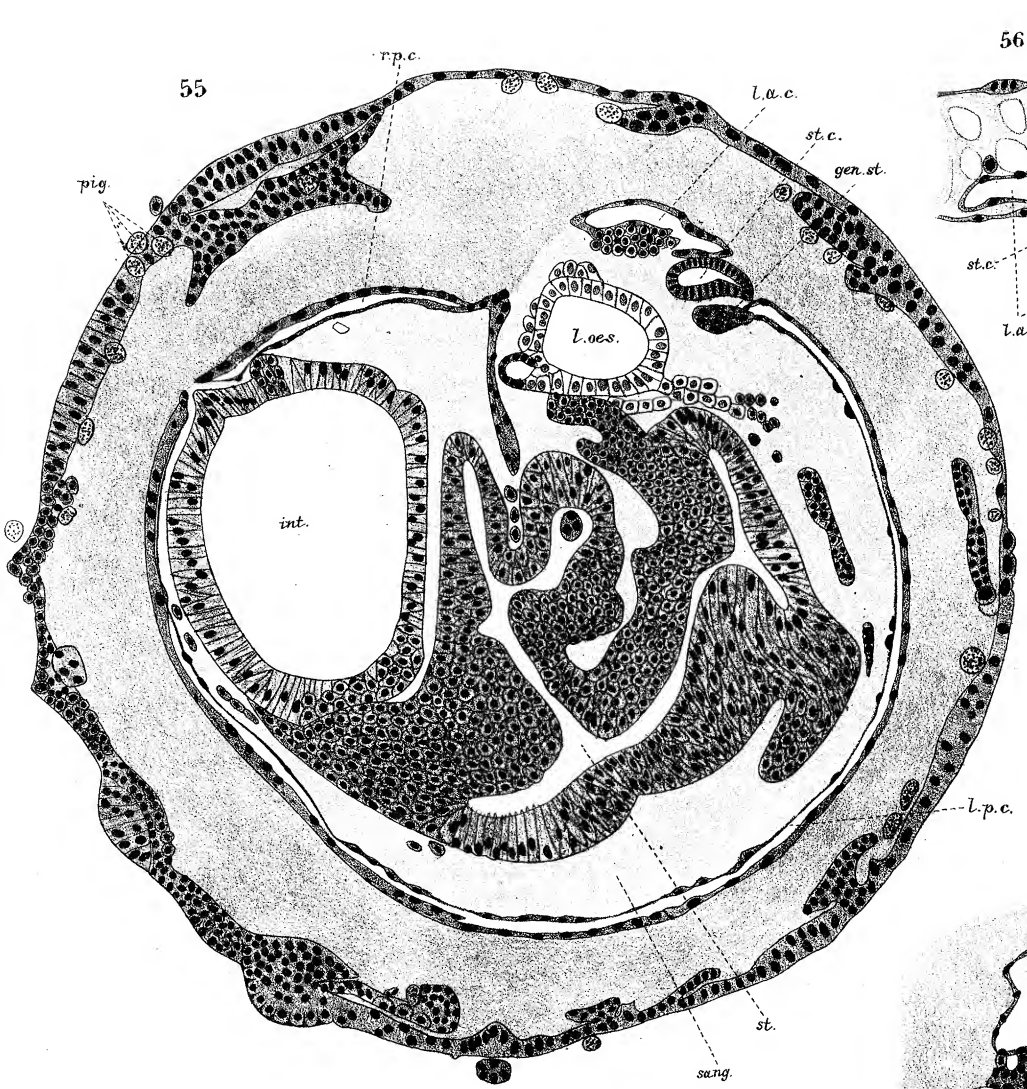
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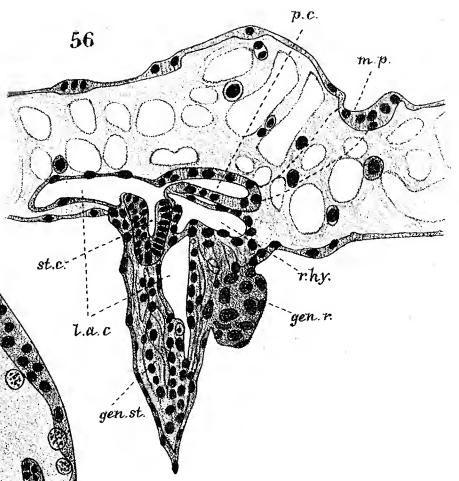
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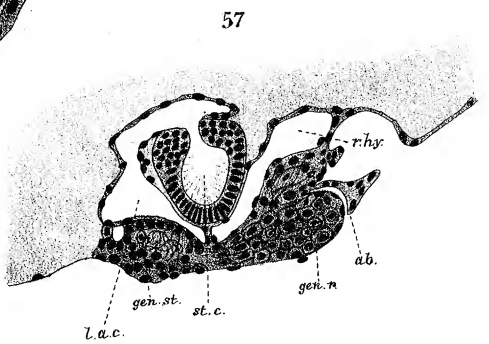
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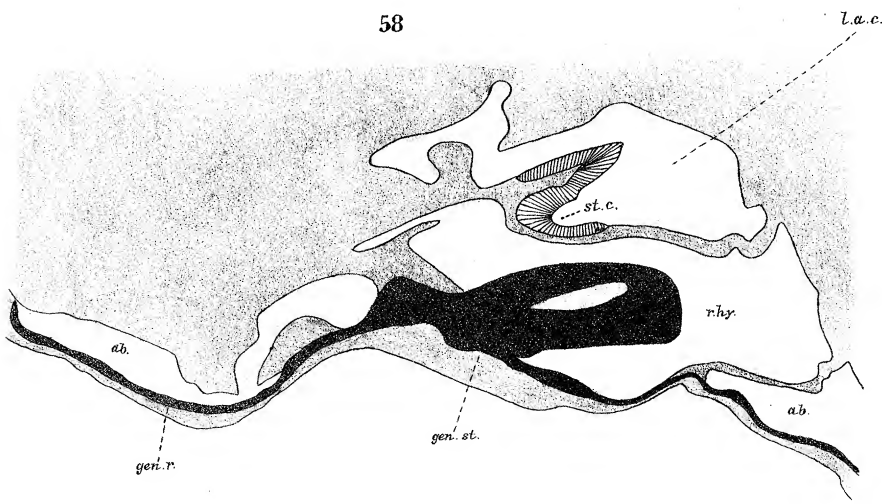
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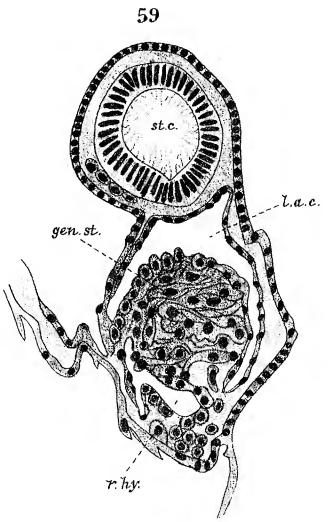
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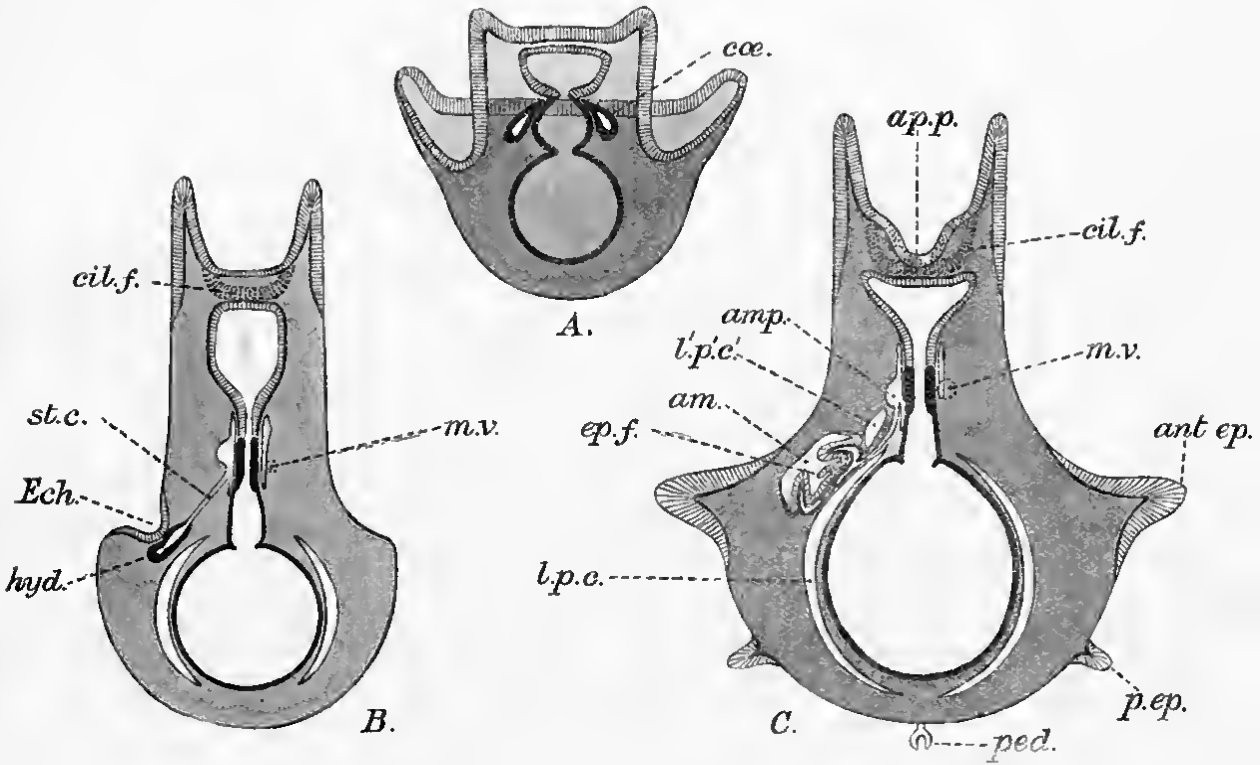


Fig. 2.—Three diagrammatic frontal sections through larvæ of different ages to show the development of echinopluteus. *A* represents an optical section, *B* and *C* actual sections. *A* through a larva 4 days old; *B* through a larva of 18 days; *C* through a larva 24 days old; *am.*, amniotic cavity; *ap.p.* apical plate; *cil.f.*, frontal cilia; the position of the ciliated band corresponds to the frontal loop of the Asteria larva. *Ech.*, invagination about to form oral disc of adult; *l.p.c.*, *l' p' c'*, the two horns of the left posterior cœlom; *m.v.*, right hydrocœle.

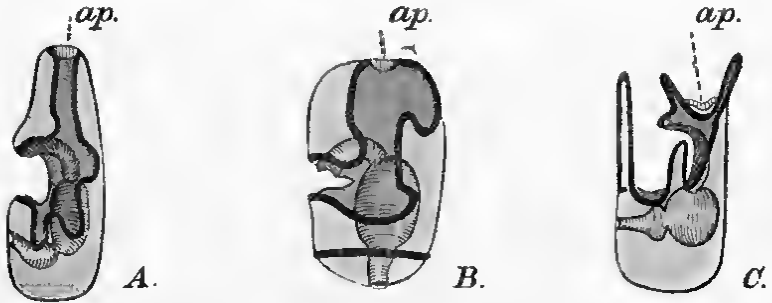


Fig. 3.—Three diagrams representing the side views of the Bipinnaria, the Tornaria, and the Echinopluteus larvæ respectively. *A* the Bipinnaria; *B* the Tornaria; *C* the Echinopluteus. The ciliated band is represented by a heavy line, and in the Echinoplnteus the præ-oral loop of the ciliated band is very short. *ap.*, the apical nervous system.

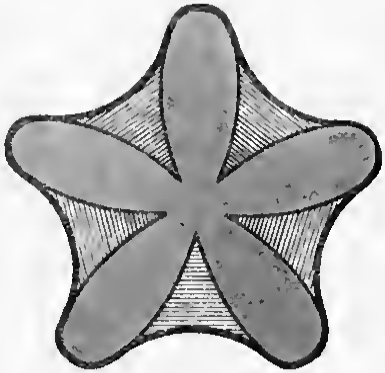


Fig. 4.—Plan of the Echinus-rudiment at about 24 days, viewed from the outside. The cross-hatched wedges are the epineural folds.

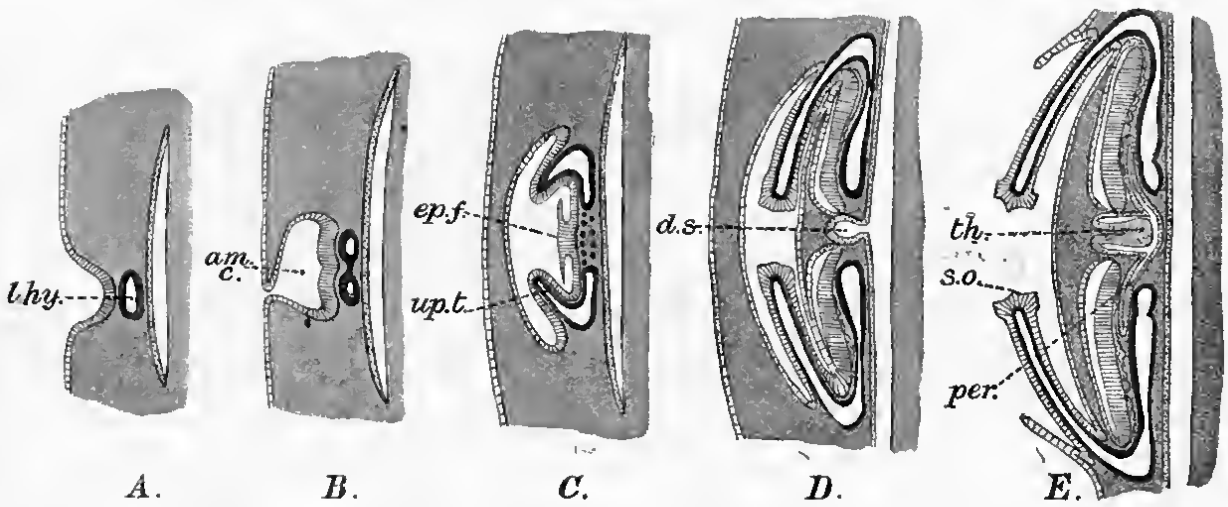


Fig. 5.—Five diagrams to show the gradual growth and differentiation of the echinus-rudiment. *am. c.* amniotic cavity; *d. s.*, dental sac; *ep. f.*, epineural fold; *l. hy.*, left hydrocœle; *per.*, rudiment of the perihæmal canal of the adult; *s. o.*, sense organ on apex of tube-foot; *th.*, rudiment of tooth; *up. t.*, unpaired tube-foot.

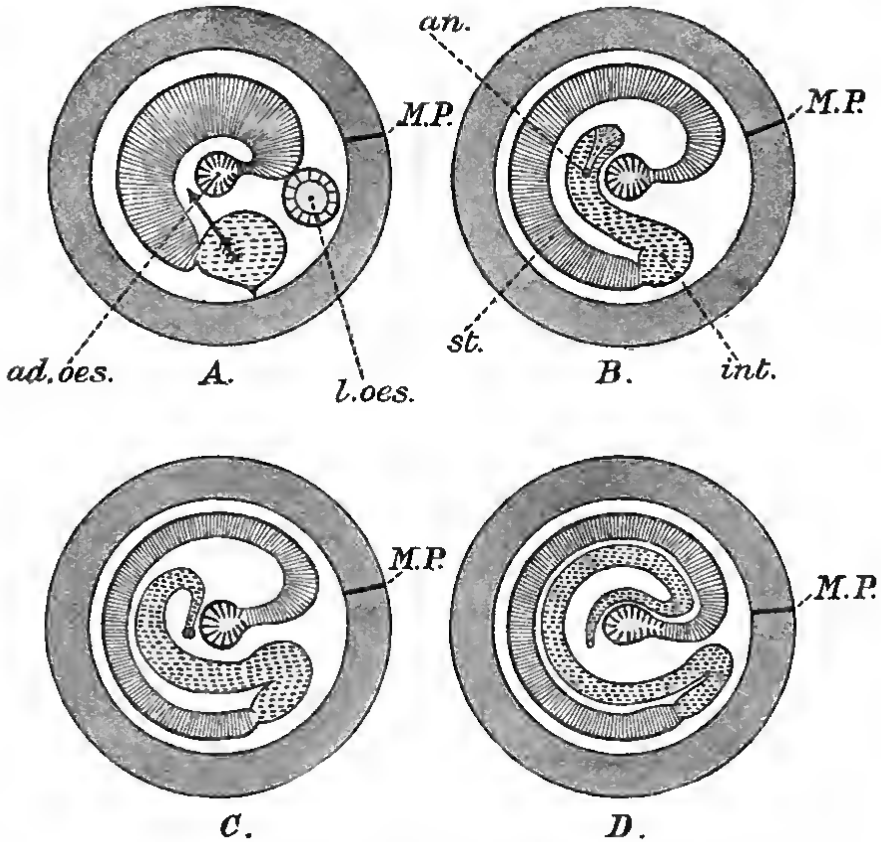


Fig. 6.—Four diagrams showing the manner in which the larval gut is transferred into the adult alimentary canal; *ad. œs.*, adult œsophagus; *l. œs.*, larval œsophagus; *an.*, annas; *int.*, intestine; *st.*, stomach; M.P., interradius in which the madreporite is situated. The arrow in diagram A shows the direction in which the anus migrates.

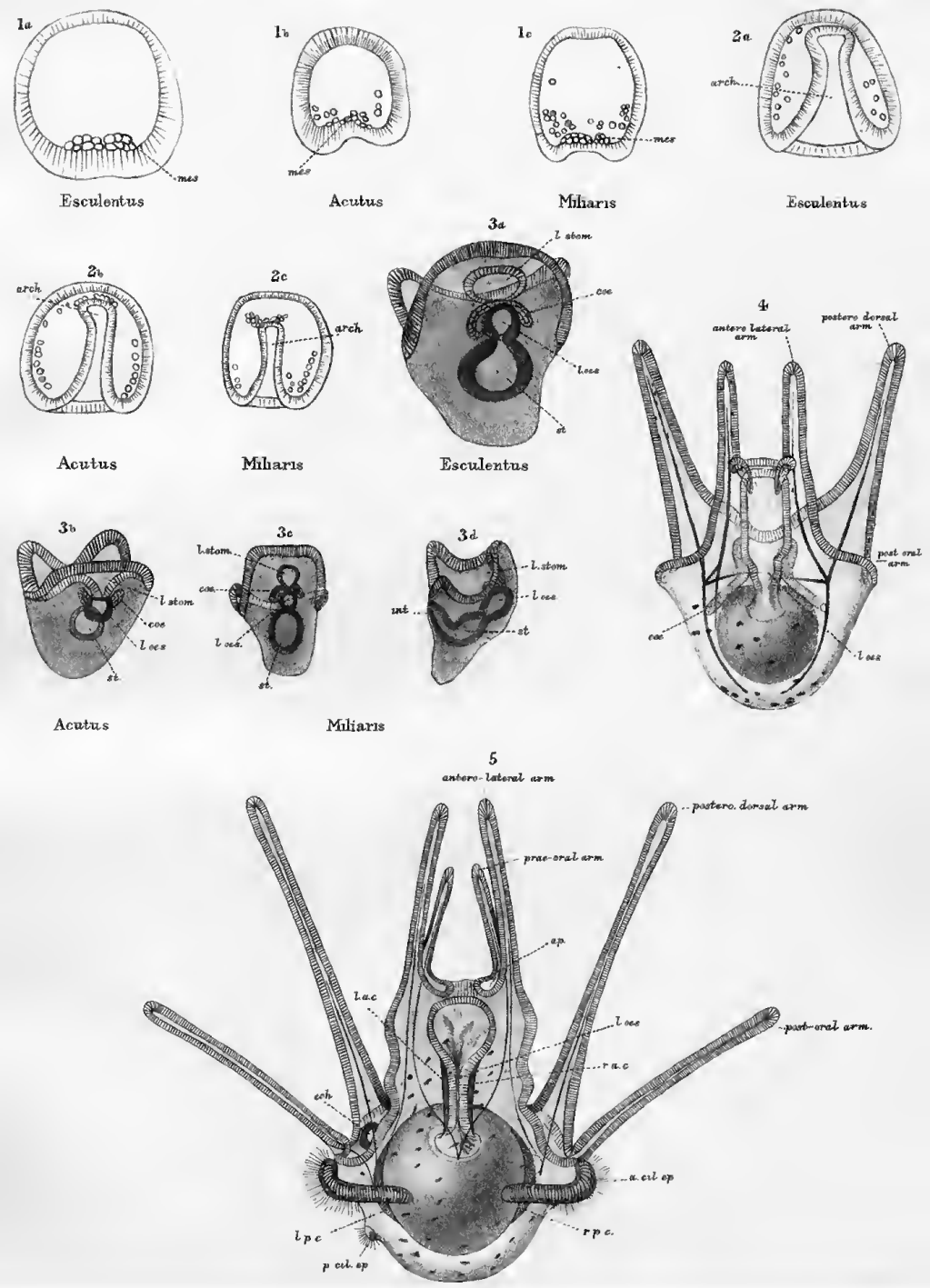


PLATE 7.

Figs. 1*a*, 1*b*, 1*c*. Optical sections of the blastulæ of *Echinus esculentus*, *E. acutus*, and *E. miliaris* respectively, magnified 200 diameters. *mes.*, primary mesenchyme cells.

Figs. 2*a*, 2*b*, 2*c*. Optical sections of the gastrulæ of *Echinus esculentus*, *E. acutus*, and *E. miliaris* respectively. Magnification the same as before. *arch.*, archenteron.

Figs. 3*a*, 3*b*, 3*c*. The larvæ of *Echinus esculentus*, *E. acutus*, and *E. miliaris* respectively, at the age of 3 days, viewed from in front. Fig. 3*d* the larva of *E. miliaris* of the same age, viewed from the side. Magnification the same as before. *cœ.*, primary cœlomic vesicle. *l. stom.*, larval stomodæum, not as yet united to the œsophagus.

Fig. 4. Larva of *Echinus esculentus*, about 7 days old, viewed from in front. Magnified 90 diameters.

Fig. 5. Larva of *Echinus esculentus*, about 23 days old, viewed from in front. Magnification as in fig. 4. *a.p.*, apical plate of neuro-epithelial cells. *a. cil. ep.*, the anterior ciliated epaulettes which are first formed. *p. cil. ep.*, the posterior ciliated epaulette just forming. *ech.*, the ectodermic invagination, the floor of which will form the oral disc of the future Echinus.

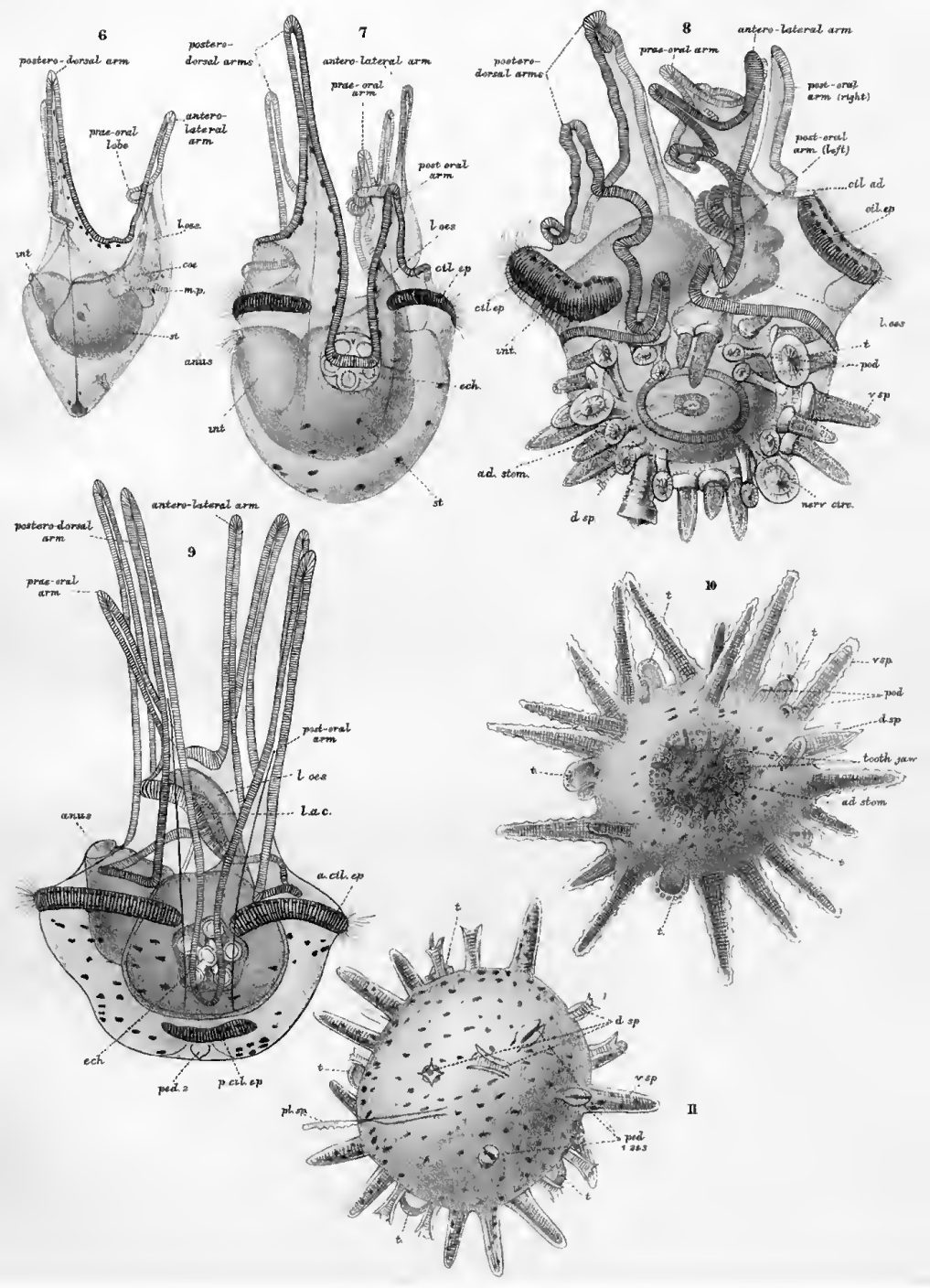


PLATE 8.

Fig. 6. Side view of a larva of *Echinus miliaris*, about 6 days old. Magnified 90 diameters. *m.p.*, primary madreporic pore.

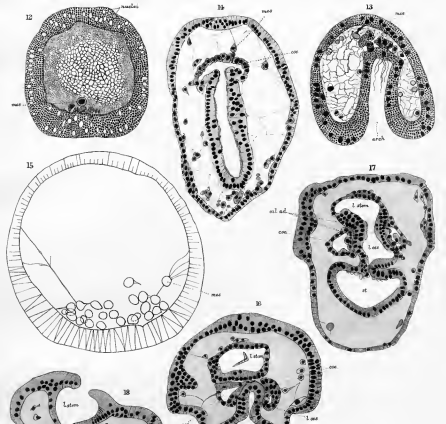
Fig. 7. Side view of a larva of *Echinus miliaris*, about 22 days old; *cil. ep.*, the ciliated epaulette. *Ech.*, the rudiment of the oral disc of the future urchin. Magnified 90 diameters.

Fig. 8. Side view of a larva of *Echinus miliaris* in the act of metamorphosis: the "arms," *i.e.*, the processes of the main ciliated band, are already shrivelling. Magnification 125 diameters. *t.*, primary unpaired tube-feet of the young urchin. *pod.*, the paired tube-feet. *v. sp.*, ventral spine. *d. sp.*, quadrate dorsal spine. *nerv. circ.*, nerve ring. *ad. stom.*, adult stomodæum forming beneath the epineural veil.

Fig. 9. Side view of a larva of *Echinus esculentus*, about 27 days old. *ped.* 2, the dorsal pedicellaria. Magnified 90 diameters.

Fig. 10. Ventral view of a just metamorphosed specimen of *Echinus esculentus*. Magnification 90 diameters.

Fig. 11. Dorsal view of a just metamorphosed specimen of *Echinus esculentus*. Magnification 90 diameters. *pl. sp.*, remnant of the skeleton of one of the "arms" of the larva.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ect

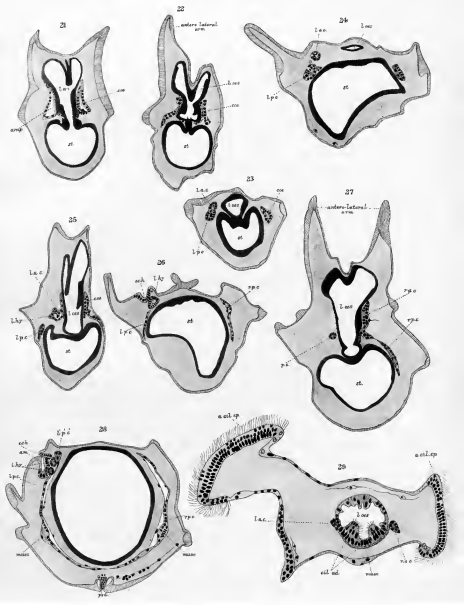

PLATE 10.

(All the figures on this plate refer to *Echinus esculentus*.)

Fig. 21. Horizontal section of a larva 5 days old. Magnification about 200 diameters. *amp.*, ampulla of the stone-canal formed from the left anterior cœlom.

Fig. 22. Horizontal section of a larva about 6 days old. Magnification the same as in foregoing figure. The cœlomic sacs are beginning to extend backwards along the stomach.

Fig. 23. Horizontal section of a larva 8 days old. Magnification as before. The left cœlomic sac is just dividing into anterior and posterior portions.

Fig. 24. Horizontal section of a larva 8 days old, but more advanced in development than that represented in fig. 23. Magnification as before. The division of the left cœlomic sac is complete.

Fig. 25. Horizontal section of a larva 9 days old, showing the formation of the left hydrocœle from the left anterior cœlomic sac. Magnification as before. *l.hy.*, incipient hydrocœle separated from the anterior cœlom only by a constriction.

Fig. 26. Horizontal section of a larva about 11 days old, showing the completely formed left hydrocœle and the ectodermic invagination growing inwards to meet it. Magnification as before. *œk.*, the invagination of the ectoderm, which will form the future oral surface of the sea-urchin.

Fig. 27. Horizontal section of a larva 12 days old, showing the division of the right cœlomic cavity into anterior and posterior portions. Magnification as before. *p.c.*, the pore-canal leading to the primary madreporic pore cut transversely.

Fig. 28. Horizontal section of a larva 21 days old, showing the division of the left hydrocœle into lobes, and the moulding of the ectodermic invagination on these lobes. Magnification as before. *l'p.c.'*, the anterior horn of the posterior division of the left cœlomic sac extending in front of the hydrocœle so as ultimately to completely encircle it. *Musc.*, muscular fibrils developed from the walls of the cœlomic sacs in order to move the skeletal rods supporting the "arms."

Fig. 29. Transverse section of a larva 22 days old, through the œsophagus. Magnified 360 diameters. *musc.*, transverse muscular fibres running from the right to the left anterior cœlomic sac, and serving to constrict the œsophagus.

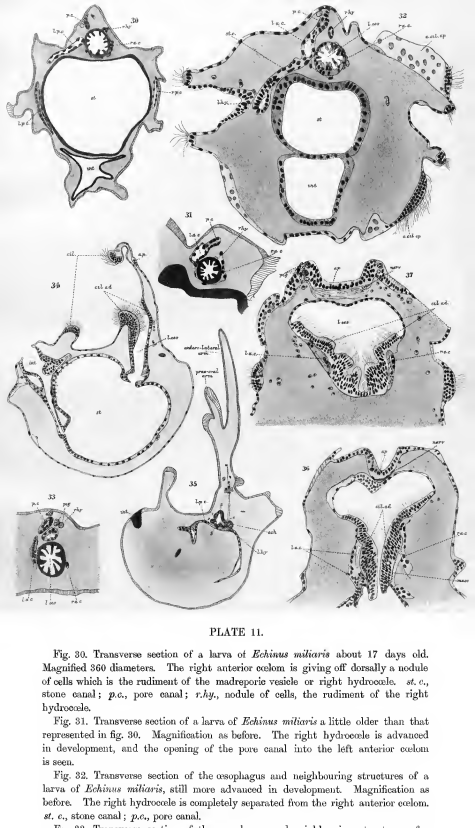

PLATE 11.

Fig. 30. Transverse section of a larva of *Echinus miliaris* about 17 days old. Magnified 360 diameters. The right anterior cœlom is giving off dorsally a nodule of cells which is the rudiment of the madreporic vesicle or right hydrocœle. *st. c.*, stone canal; *p.c.*, pore canal; *r.hy.*, nodule of cells, the rudiment of the right hydrocœle.

Fig. 31. Transverse section of a larva of *Echinus miliaris* a little older than that represented in fig. 30. Magnification as before. The right hydrocœle is advanced in development, and the opening of the pore canal into the left anterior cœlom is seen.

Fig. 32. Transverse section of the œsophagus and neighbouring structures of a larva of *Echinus miliaris*, still more advanced in development. Magnification as before. The right hydrocœle is completely separated from the right anterior cœlom. *st. c.*, stone canal; *p.c.*, pore canal.

Fig. 33. Transverse section of the œsophagus and neighbouring structures of a larva of *Echinus miliaris*, about 20 days old. Magnification as before. The right hydrocœle has become a hollow vesicle. *pig.*, pigment-bearing wandering cells.

Fig. 34. Median sagittal section of a larva of *Echinus esculentus*, 20 days old. Magnification 200 diameters. *ap.*, first trace of ectodermic thickening, out of which neuro-epithelial apical plate is developed.

Fig. 35. Lateral sagittal section of a larva of *Echinus esculentus*, 19 days old. Magnification as in fig. 34. The formation of lobes on the left hydrocœle is seen. *ect.*, the ectoderm invagination which becomes applied to the hydrocœle out obliquely. 1, 2, 3, 4, 5, the lobes of the left hydrocœle.

Fig. 36. Horizontal section through the œsophagus and neighbouring structures of a larva of *Echinus esculentus*, 24 days old. Magnification 360 diameters. *nerv.*, the first nerve fibrils formed under the rudimentary apical plate. *musc.*, the transverse muscles of the larval œsophagus cut across.

Fig. 37. Horizontal section through the œsophagus and neighbouring structures of a larva of *Echinus esculentus*, 50 days old, just about to metamorphose. Magnification the same as in fig. 36. The apical plate (*ap.*) has reached the full development, and has a thick mass of nerve fibrils beneath it.

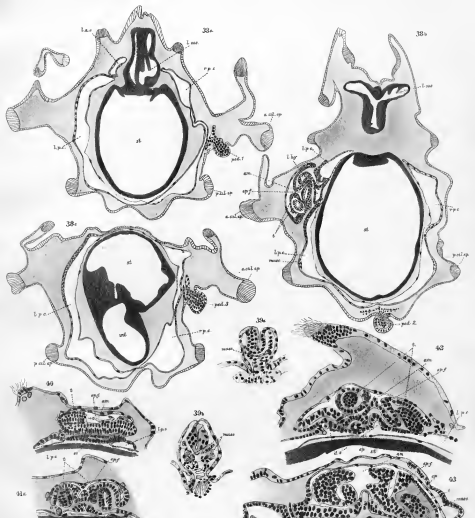

PLATE 12.

Figs. 38*a*, *b*, &c. Three horizontal sections through a larva of *Echinus esculentus*, 26 days old. Magnified 200 diameters. In each of the sections one of three primitive pedicellariæ is seen to be developing as a rounded nodule. In fig. 38*b* the primary outgrowths of the hydrocœle (*l*) are seen projecting into the amniotic space, and the epineural fold has been developed so as to cover the original surface of the oral disc of the future sea-urchin. The left posterior cœlom has completely surrounded the hydrocœle, as is shown by the position of its anterior horn, *l' p' c'*. In fig. 38*c* the right and left posterior cœlomic sacs are seen to come into contact with one another beneath the intestine.

Figs. 39*a* and *b*. Two stages in the development of a pedicellaria. Magnified 360 diameters. Fig. 39*a* is taken from a larva of *E. esculentus* about 26 days old, fig. 39*b* from one about 30 days old. The muscles, *musc.*, moving the blades are seen to be developed from wandering cells.

Fig. 40. Horizontal section through the hydrocœle and associated structures of a larva of *Echinus miliaris*, about 25 days old. Magnification 360 diameters. *am.*, amniotic space. *ep. f.*, rudimentary epineural fold.

Figs. 41*a* and *b*. Two horizontal sections through the hydrocœle and associated structures of a larva of *Echinus miliaris* slightly more advanced than that represented in fig. 40. Magnification 360 diameters.

Fig. 42. Horizontal section through the hydrocœle and associated structures of a larva of *Echinus esculentus*, 29 days old. Magnification 360 diameters. *d.s.*, invaginations of the epithelium of the left posterior cœlom which form the rudiments of the dental sacs and the teeth.

Fig. 43. Horizontal section through the hydrocœle and associated structures of a larva of *Echinus esculentus*, 30 days old. Magnification 360 diameters. The dental sac is just being separated from the cœlom. The thickening in its outer wall is the first trace of the tooth. *nerv.*, the nervous fibrils of the developing nerve ring of the adult. *musc.*, muscular fibres developing from the cells of the part of the hydrocœle contained in the primary unpaired tube-feet. (*l.*)

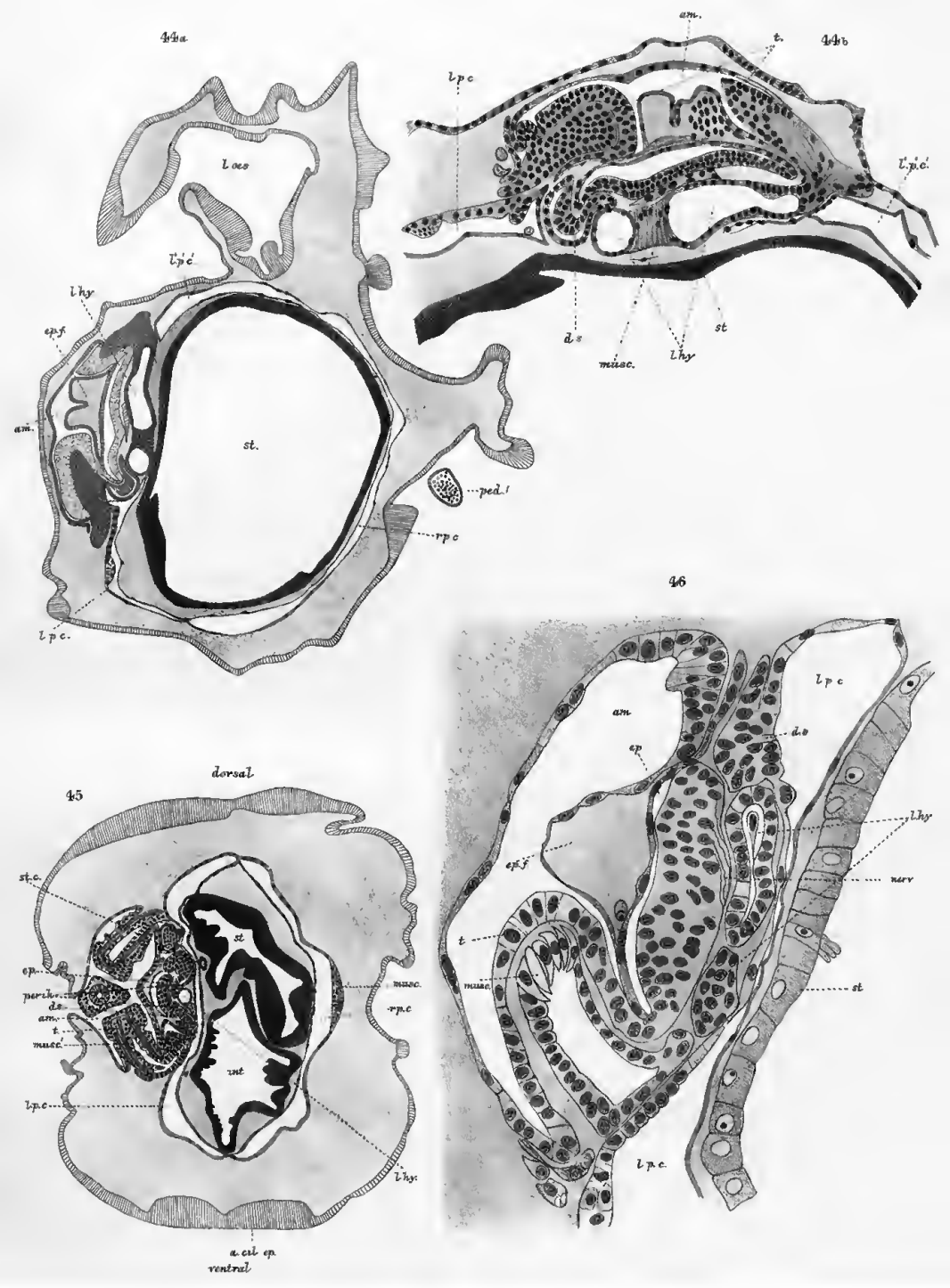

PLATE 13.

(All the figures in this plate refer to *Echinus esculentus*.)

Figs. 44*a* and *b*. Two figures of a frontal section through a larva, 29 days old. Fig. 44*a* shows the whole section. Magnified 200 diameters. Fig. 44*b*, the hydrocœle and adjoining structures. Magnified 360 diameters. *musc.*, circular muscles surrounding the hydrocœle and derived from its epithelial cells. *d.s.*, a completely closed dental sac with the rudiment of the tooth projecting into it.

Fig. 45. Transverse section of a larva, 36 days old. Magnified about 140 diameters. *a.m.*, amniotic space now open to the exterior. *perih.*, perihæmal outgrowth of the dental sac (*d.s.*) arching over a lobe of the hydrocœle, *l. hy.*

Fig. 46. Horizontal section through the hydrocœle and associated structures of a larva, 29 days old. Magnified 1000 diameters, in order to show the first trace of the adult nervous system. *nerv.*, the first nervous fibrillæ formed from the ectoderm of the rudiment of the oral disc of the adult. *musc.*, epithelial cells forming part of the wall of the hydrocœle in the first stage of conversion into muscles.

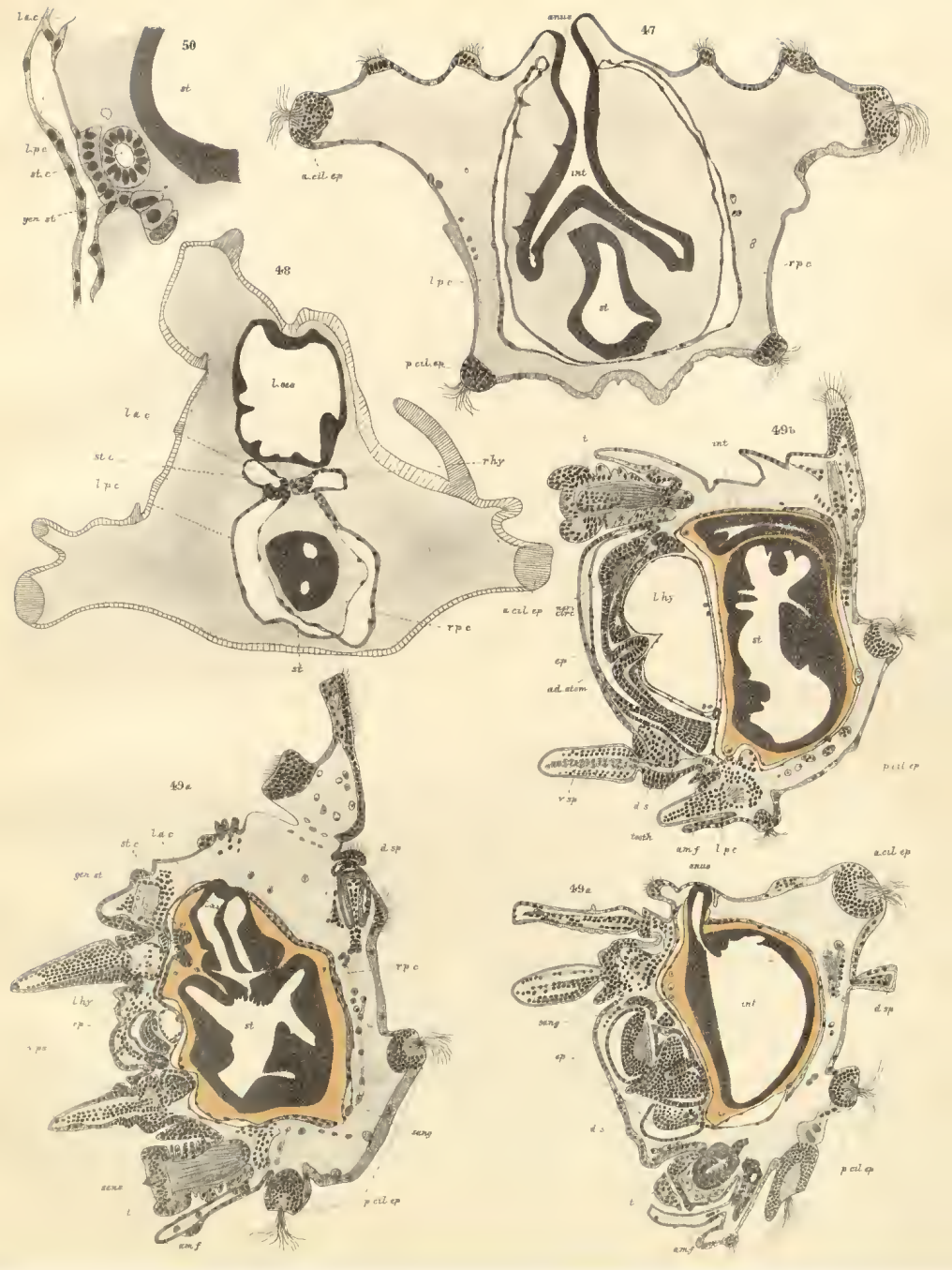

PLATE 14.

(All the figures in this plate refer to *Echinus esculentus*.)

Fig. 47. Horizontal section through a larva, 33 days old, in the region of the anus. Magnified 200 diameters. *p. cil. ep.*, posterior ciliated epaulette. *r.p.c.*, *l.p.c.*, right and left posterior cœlomic sacs respectively, meeting each other beneath the stomach.

Fig. 48. Horizontal section through a larva, 30 days old, in the region of the œsophagus. Magnified 200 diameters. *st. c.*, stone-canal, opening into the left anterior cœlom, the so-called "ampulla" of the stone-canal. *r. hy.*, the right hydrocœle or madreporic vesicle.

Figs. 49*a*, *b*, *c*. Three horizontal sections through a larva about 42 days old, which, whilst still retaining its ciliated bands, was crawling on the bottom by means of its primary tube-feet. Magnification, 200 diameters. Fig. 49*a* is through the region of the larval œsophagus; fig. 49*b* through the region of the adult stomodæum; fig. 49*c* through the vanishing larval anus. *am. f.*, amniotic fold, the remnant of the roof of the amniotic cavity now freely open to the exterior. *d. sp.*, the first blunt clavate spines of the dorsal regions of the adult. *v. sp.*, the pointed spines of the ventral surface of the adult. *sang.*, the modified jelly surrounding the stomach which gives rise to the so-called "blood-vessels" of the adult. *ad. stom.*, the adult stomodæum arising from the floor of the epineural space. *gen. st.*, the first trace of the genital stolon.

Fig. 50. A small portion of the same section as that represented in fig. 49*b*. Magnified 750 diameters. *st. c.*, stone-canal. *gen. st.*, genital stolon.

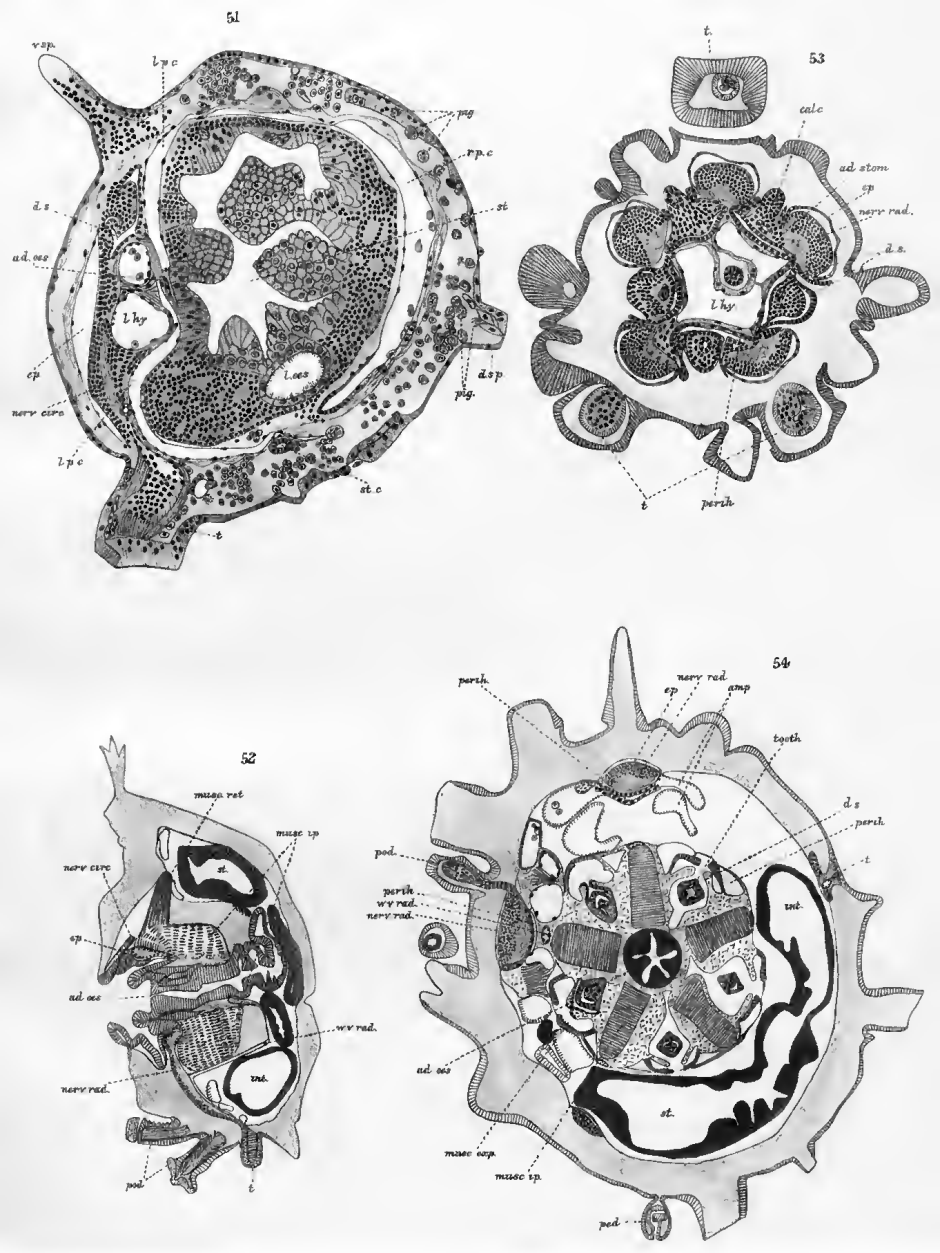

PLATE 15.

Fig. 51. Transverse section through a young sea-urchin which has just completed its metamorphosis. Magnification 200 diameters. *st.*, stomach, the epithelium of which is rounding itself off into spherical cells and budding off these profusely into the surrounding jelly; this is the process known as histolysis. *l. œs.*, vestige of the fast-disappearing larval œsophagus. *ad. œs.*, first trace of an outgrowth from the stomach which will meet the adult stomodæum (which is not in the plane of the figure), and so complete the adult œsophagus. *pig.*, pigment-bearing amœbocytes engaged in devouring the invaginated pieces of larval ectoderm. *nerv. circ.*, the nerve ring of the adult now formed.

Fig. 52. Transverse section through a young sea-urchin 7 millims. in diameter. Magnification 90 diameters. The terminal tentacle or unpaired primary tube-foot still projects freely, but has been shifted (as compared with the corresponding structure in fig. 51) dorsally owing to the greater growth of the oral surface. *pod.*, the first paired tube-feet now larger than the unpaired one. *w.v. rad.*, the radial water vascular canal. *musc. i.p.*, the interpyramidal muscles of Aristotle's lantern connecting one jaw with the other. *musc. ret.*, the retractor muscles of the jaws. *nerv. rad.*, the radial nerve.

Fig. 53. Section through a young sea-urchin, which has just completed its metamorphosis, taken parallel to the disc. Magnified 360 diameters. *perih.*, rudiment of the perihæmal radial canal, which is seen to be an outgrowth of the tooth sac.

Fig. 54. Section parallel to the disc of a sea-urchin. ·57 millim. in diameter. Magnified 200 diameters. *amp.*, ampulla of one of the paired tube-feet. The perihæmal cavities are now cut off from those of the tooth-sacs.

PLATE 16.

Fig. 55. Section parallel to the disc of a young *Echinus esculentus* which has just completed its metamorphosis. Magnification 360 diameters. The section shows the larval œsophagus and the larval intestine in their relation to the stomach.

Fig. 56. Section parallel to the disc through the genital stolon and adjoining structures in a young sea-urchin 65 millims. in diameter. Magnification 720 diameters. The outline of the pore-canal (*p.c.*) leading from the still single madreporic pore (*m.p.*) to the left anterior cœlom or ampulla of the stone-canal (*l a.c.*) does not lie completely in the plane of the figure and is consequently dotted for part of its course. *gen. r.*, rudiment of the genital rachis.

Fig. 57. Section parallel to the disc through the genital stolon and adjoining structures of a young sea-urchin (probably *Echinus microtuberculatus*) 1·28 millims. in diameter. Magnification 360 diameters. *ab.*, first trace of the aboral sinus, an extension of the cœlom surrounding the genital rachis.

Fig. 58. Section parallel to the disc through the genital stolon and adjoining structures of a young sea-urchin (*sp.*) 6·5 millims. in diameter. Magnification 200 diameters. The genital rachis is (*gen. r.*) completely formed, and is enveloped in the aboral sinus (*ab.*).

Fig. 59. Another section parallel to the disc of the same specimen as that represented in fig. 58, through the stone-canal and genital stolon. Magnification 360 diameters.